

Lateralised repetition priming for face recognition: priming occurs in the right hemisphere only

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PERCEPTION
VOLUME 32 SUPPLEMENT



26 EUROPEAN CONFERENCE ON VISUAL PERCEPTION

Paris, 1 – 5 September 2003

Abstracts

Twenty-six European Conference on Visual Perception

Paris, France

1 – 5 September 2003

Abstracts

SYMPOSIA AND ORAL PRESENTATIONS

MONDAY

The *Perception* lecture (P Cavanagh) 1

TUESDAY

INVITED SYMPOSIUM 1

Algorithmic and biological vision 1

INVITED SYMPOSIUM 2

Attention and decision processes 3
in visual perception

ORAL PRESENTATIONS

Learning, memory, development, and 5
ageing

Multisensory perception 8

Action and perception, vection, optic 10
flow

Binocular vision, depth, stereo and 12
space perception

WEDNESDAY

INVITED SYMPOSIUM 3

Multisensory and sensorimotor 15
interactions

INVITED SYMPOSIUM 4

Neuropsychology of visual extinction 17

ORAL PRESENTATIONS

Motion—low level 19

Eye movements and perception 22

Objecthood 1 25

THURSDAY

INVITED SYMPOSIUM 5

Perceptual learning 29

INVITED SYMPOSIUM 6

The experience of seeing: physiology, 31
psychophysics, and philosophy

ORAL PRESENTATIONS

Motion—high level 33

Clinical 36

Colour (in memory of Dick Cavonius) 38

Lightness, brightness, shading, 40
transparency 1

FRIDAY

ORAL PRESENTATIONS

Attention and awareness 43

Low-level processes 46

Top – down, bottom – up, and sideways 49
interactions (in honour
of Richard Gregory)

Lightness, brightness, shading, 51
transparency 2

Natural images 54

Face perception 56

Objecthood 2 58

POSTERS

TUESDAY

Action, self-motion, optic flow, and 61
space perception

Binocular vision, stereo, depth and 73
space perception

Development and ageing, learning, 85
and memory

Cross-modal interactions 94

WEDNESDAY

Motion—low level 100

Eye movements and perception 107

Objecthood 114

Ambiguous perception, illusions, and art 123

Attention 1 131

THURSDAY

Attention 2 139

Motion—high level 142

Low-level processes—colour 146

Lightness, brightness, shading, 150
transparency

Low-level processes—spatiotemporal 156
aspects

From neurons to phenomenology 166

Natural scenes 168

Face perception 172

Clinical 175

Author index 181

APPERCEPTIONS—A colour 16-page guide to the art exhibition staged in conjunction with ECVP03 follows the Author index

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ECVP '03 Abstracts

MONDAY

THE PERCEPTION LECTURE

◆ The language of vision

P Cavanagh (Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA; e-mail: patrick@wjh.harvard.edu)

One role of visual attention is the construction of a visual narrative, a description of visual events in a language-like format. Recent work on the architecture of attention shows that it has simultaneous access to multiple selections, and luckily so, because other studies show that it is impossible to scrutinise the details within a single selection. As a result, the integration of elements, the derivation of their relations, and the actions they are engaged in is only possible by comparing information across multiple selections. The product of this cross-selection is a language-like description of the visual event that is then exported to other modules in the brain. A basic distinction immediately arises between objects ('nouns') that can be selected rapidly with a single operation, and actions ('verbs') that always require multiple selections. Results from parietal patients demonstrate a candidate case of syntax for motion and transient events.

[Supported by NIH EY09258.]

TUESDAY

INVITED SYMPOSIUM 1

ALGORITHMIC AND BIOLOGICAL VISION: POINTS OF ENCOUNTER

◆ Selection of kernel location, frequency, and orientation parameters of 2-D Gabor wavelets for face recognition

B Gokberk, L Akarun, E Alpaydin (Department of Computer Engineering, Bogazici University, PK 2, TR 34342 Bebek, Istanbul, Turkey; e-mail: gokberk@boun.edu.tr)

In local feature-based face-recognition systems, the topographical locations of feature extractors directly affect the discriminative power of a recogniser. Better recognition accuracy can be achieved by the determination of the positions of salient image locations. Most of the facial-feature-selection algorithms in the literature work with two assumptions: one, that the importance of each feature is independent of the other features; and, two, that the kernels should be located at fiducial points. Under these assumptions, one can only get a suboptimal solution. Here, we present a methodology that tries to overcome this problem by relaxing the two assumptions by using a formalism of subset selection problem. In addition to the topographical information, resolution and orientation are also the two important parameters of a feature extractor, since face contains features having different orientation and resolution. Therefore, it is natural to design a feature extractor which takes into account these characteristics of faces. Among several alternatives, 2-D Gabor wavelets are very suitable for this task. The selection of resolution and orientation parameters at specific face locations is also carried out by a supervised sequential floating subset search. This step concludes our two-level feature selection methodology, in which the first step extracts topographical importance, and the second step extracts frequency and orientation information. Experiments on the FERET data set are presented, and the validity of the approach is discussed.

◆ Non-classical receptive field inhibition and contour detection

N Petkov, M A Westenberg, C Grigorescu (Institute of Mathematics and Computing Science, University of Groningen, PO Box 800, NL 9700 AV Groningen, The Netherlands; e-mail: petkov@cs.rug.nl; website: www.cs.rug.nl/~petkov)

Various visual effects show that the perception of an edge or a line can be influenced by other such stimuli in the surroundings. Such effects can be related to non-classical receptive field (non-CRF) inhibition that is found in 80% of the orientation-selective neurons in the primary visual cortex (Nothdurft et al, 1999 *Visual Neuroscience* **16** 15–34). A mathematical model of non-CRF inhibition is presented in which the response of an orientation-selective cell is suppressed by the responses of other such cells beyond its classical (excitatory) receptive field. Non-CRF inhibition acts as a feature contrast computation for oriented stimuli: the response to an optimal stimulus over the receptive field is suppressed by similar stimuli in the surround.

Consequently, it strongly reduces the responses to texture edges while scarcely affecting the responses to isolated contours. The biological utility of this neural mechanism might thus be that of contour (versus texture) detection. Two types of inhibition are considered—isotropic and anisotropic—that respectively, do and do not depend on the orientation difference of centre and surround stimuli. The results of computer simulations based on the proposed model explain perceptual effects, such as orientation contrast pop-out, ‘social conformity’ of lines embedded in gratings, reduced salience of contours surrounded by textures, and decreased visibility of letters embedded in band-limited noise (Petkov and Westenberg, 2003 *Biological Cybernetics* **88** 236–246). The insights into the biological role of non-CRF inhibition can be utilised in machine vision. The proposed model is employed in a contour-detection algorithm that substantially outperforms previously known such algorithms in computer vision (Grigorescu et al, 2003 *IEEE Transactions on Image Processing* **12** 729–739).

◆ **Acquiring visual object concepts**

P Sinha (Brain and Cognitive Sciences, Massachusetts Institute of Technology, E25-229, 45 Carleton Street, Cambridge, MA 02142, USA; e-mail: sinha@ai.mit.edu)

Understanding how the human visual system learns to perceive objects in the environment is a fundamental challenge in neuroscience. Through experience, the brain comes to be able to parse complex visual scenes into distinct objects. Several questions about this process remain unanswered. How much visual experience is needed for the development of this ability? What are the intermediate stages in the evolution of the object representations? How critical is early visual experience for the development of object perception? These questions are addressed by studying a unique population of children—those who have recovered sight after several years of visual deprivation. The goal is to characterise the timeline of object concept acquisition by the children and to use the results to develop and constrain computational models. Here I focus on the acquisition of the basic face-versus-non-face discrimination skill. I report studies with two children, both of whom suffered from congenital blindness lasting at least the first seven years of life. Their face classification skills were assessed after surgical restoration of sight. For one child, the experiments were performed 1.5 months after surgery, and for the other, four years after surgery. The results indicate that these children are able to detect faces and distinguish them from distractors with high reliability comparable to control subjects. Furthermore, this ability appears to be based on the use of overall facial configuration rather than individual features—a finding that presents an interesting contrast to the hypothesis of piecemeal processing used to explain impairments in face identification. A computational model of face concept learning that incorporates these findings is being developed.

◆ **Fechner revisited**

J J Koenderink (Buys Ballot Laboratory, Utrecht University, Princetonplein 5, NL 3584 CC Utrecht, The Netherlands; e-mail: j.j.koenderink@phys.uu.nl)

Fechner’s ‘psychophysical law’ states that the natural intensity scale is logarithmic. This has evoked many ‘explanations’, most of them having to do with Weber’s law, ecological optics (independence of absolute level of illumination), or optimal channel capacity. I show that a totally different interpretation is possible. This interpretation is somewhat in the sense of Fechner as it identifies the ‘natural’ structure. I generalise the law to regions of the visual field in order to be able to describe spatial structure: then the problem of comparison of intensities at different locations arises. One needs a formal structure that accounts for the many familiar ‘congruences’, such as brightness and contrast (gamma) changes that somehow leave the image invariant. The solution to this problem is a Cayley–Klein geometry with one isotropic dimension. The aforementioned congruences are the motions of this space. One obtains a very general framework that is of immediate use in image processing (algorithmic vision) and may serve as a model of the visual field (biological vision).

◆ **Functional geometry of the visual areas**

J Petitot (CREA, École Polytechnique, 1 rue Descartes, F 75005 Paris, France; e-mail: petitot@poly.polytechnique.fr)

I present a geometrical model of the functional architecture of area V1 and, more precisely, of its pinwheel structure. The problem is to understand from within how the internal geometry of the visual cortex can produce the geometry of the external space. It is shown that the horizontal cortico-cortical connections of V1 implement what the geometers call a contact structure and a Frobenius integrability condition. Three applications are then developed to the psychophysical concept of association field (Field, Hayes, Hess), to a variational model of curved modal illusory contours, and to Ermentrout’s, Cowan’s, Bressloff’s, and Golubitsky’s model of visual hallucinations.

◆ Visual computations and visual cortex

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I consider the analysis of visual information by brains and by computers. A theory of early computational vision, from edge detection to shading and stereo, is sketched. The theory is geometrical, and is realised by identifying edge elements with a local approximation to tangents. Curvature is necessary to introduce consistency between tangents, and is thus key to understanding connections in the visual cortex. Local circuitry for these computations in primate V1 is described. The resultant models quantitatively predict the anatomy and physiology of long-range horizontal connections to second-order, and provide a formal basis for inferences about perceptual surfaces. The result is a greatly expanded view of the information processing capabilities of the first cortical visual area.

INVITED SYMPOSIUM 2

ATTENTION AND DECISION PROCESSES IN VISUAL PERCEPTION

◆ The neural basis of an attentional enhancement of visual salience by feature-similarity gain

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The strength of visual stimuli relative to other stimuli and the background, ie their salience, is a central determinant how effective a given stimulus is in attracting attention and how quickly it can be detected and discriminated. While physiological studies of attention in extrastriate cortex have demonstrated multiplicative effects of attention on neuronal responses, such influences will not change the relative strength of stimuli. Here we present data from recordings of neurons in extrastriate cortex of macaque monkeys performing attentional tasks that demonstrate two additional aspects of attentional modulation that help resolve the apparent discrepancy. One series of experiments addresses the interaction of stimulus contrast (which—since it is a feature of every stimulus—is the most important contributor to stimulus salience) and spatial attention. We were able to show that attention has the strongest influence on stimuli of intermediate contrast, which supports the hypothesis that attention increases apparent stimulus contrast. In a second series of experiments, we investigated the influence of feature-based attention on population responses to visual stimuli. We were able to demonstrate that, in accordance with the predictions of the feature-similarity gain model of attention (Treue and Martinez Trujillo, 1999 *Nature* **399** 575–579), the activity of neurons preferring the attended feature was enhanced while the activity of neurons with the opposite preference was suppressed, in effect enhancing the salience of stimuli possessing attended features. Together these results provide the neuronal basis for an enhanced stimulus salience by attention directed towards a spatial location and/or a particular stimulus feature.

◆ Attention in crowding and averaging

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We review the role of attention in two situations: crowding and averaging. In crowding, the role of attention is surprisingly small; in averaging, the role of attention seems to be surprisingly large. Crowding refers to the difficulty of judging an object in the periphery when objects of the same kind are nearby. Pelli et al (2003, submitted) argue that crowding represents normal feature integration, but over an inappropriately large area, including not just the object of interest. Treisman and her colleagues suggested that feature integration requires attention, but crowding research shows that this feature integration does not require attention, though Prinzmetal has shown small effects of grouping and so on. Averaging refers to a task in which multiple identical targets all convey identical information at high contrast and the observer is asked to make an objective discrimination (of orientation or speed). We call it ‘averaging’ because we presume that the observer is limited by internal noise that in principle would be independent for each target, so that optimal performance would be based on the average of separate estimates for each target. Verghese and Stone, for speed discrimination, found that humans obtained this predicted improvement only up to two objects. We have similar results for orientation discrimination. We are unsure of the explanation for this failure of summation, but our observers tell us that they are unable to attend to more than two objects.

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◆ The selection of inputs by spatial attention

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Spatial attention has been reported to modify neuronal responses either by an enhancement of contrast-gain of the stimulus or by retuning of sensitivity profiles (McAdams and Maunsell, 1999 *Journal of Neuroscience* **19** 431–441). At the overall observer level, we identified corresponding mechanisms of spatial attention as stimulus enhancement or as external noise exclusion, based on a noisy observer model of behavioural performance (the perceptual template model; Lu and Doshier, 1998 *Vision Research* **38** 1183–1198). External noise exclusion is the dominant mechanism of attention in centrally pre-cued spatial attention in multi-location displays (Doshier and Lu, 2000 *Psychological Science* **11** 139–146). Although the presence of competing locations is critical, the signal and noise content of those locations is not—attention operates on stimulus inputs in the region of target itself to exclude noise (Lu et al, 2002 *Journal of Vision* **2** 312–323). This external noise exclusion by attention must reflect retuning of the perceptual template on one or more dimensions—in spatial frequency, in space, or in time. These forms of retuning were tested in orientation-discrimination tasks under conditions with large attention effects. Spatial attention did not alter the sensitivity of the observer to external noise in different spatial-frequency bands. Attention narrowed the spatial and the temporal parameters of noise sensitivity to space–time regions more closely matching the signal stimulus. Attention by external noise exclusion alters the spatial footprint and the temporal window of information sampling but need not alter the spatial-frequency tuning.

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◆ Information use in perceptual identification

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We (Huber et al, 2001 *Psychological Review* **108** 149–182) have explored the processes that are used to identify a briefly flashed visual stimulus when (as is typical in the environment) other visual stimuli occur in reasonably close temporal and spatial contiguity. We found that the visual features of the flash and the neighbouring stimuli are confused even when the neighbours are clearly seen and identified. In addition, perhaps as a consequence, the system that evaluates the evidence for what has been flashed discounts evidence from features known to have been in the neighbours. Such behaviour is well modeled as a near-optimal Bayesian decision process. In the present research, the nature of the information used to make decisions is explored. In our tasks a target word was flashed briefly, was masked, and then two choices appeared. The flashed word could be in upper or lower case, or (in a separate experiment) green or red. The diagnostic information available to choose between the two alternatives was varied: either visual information (BRAIN–brain in the case of experiment), higher-level information (BRAIN–DRAIN), or both types of information (BRAIN–drain). When the choices differ in case or colour, one might expect better performance, because perception of the case or colour of the flash would produce correct responding. For masks containing form and/or colour information, this result was not obtained: choices differing in spelling produced better performance than choices differing in case or colour but not spelling. We have found that observers do not base their decisions on the most primitive sources of visual information (eg form, or colour), but rather on higher-level codes (eg letter names, or even higher-level codes). Is this finding due to masking, decision strategies, or attentional effects? In a series of studies we manipulated the nature of both the stimuli and the masks to identify the perceptual, attentional, and decision processes producing such findings.

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◆ A common analysis of spatial attention and response bias

J Palmer, M N Shadlen[¶] (Department of Psychology [[¶]Department of Physiology and Biophysics], University of Washington, Seattle, WA 98195-1525, USA; e-mail: jpalmer@u.washington.edu)

Spatial attention and response bias are both instances of top–down influences on visual processing. We analyse both influences from the perspective of decision theory. Spatial attention incorporates knowledge about the probability of a relevant stimulus at a particular location; similarly, response bias incorporates knowledge about the probability of a decision outcome. An ideal observer can exploit both kinds of knowledge to make decisions about sensory stimuli. Here, we

test a generalisation of the ideal observer in a motion-discrimination experiment. Observers viewed displays consisting of two patches of dynamic random dot motion and judged the direction of motion (left versus right). Coherent motion occurred in only one of the two patches. Spatial attention was manipulated by the probability of motion at a given location; response bias was manipulated by the probability of a particular direction of motion. In addition, motion strength was manipulated by varying the fraction of coherently moving dots from well below threshold to well above threshold. In short, we measured the effects of location probability, direction probability, and motion strength on both accuracy and response time. The results are consistent with the predictions of a descriptive model based on signal detection theory that generalises the ideal observer. In the model, spatial attention is mediated by a change in the relative weights given to different sources of evidence; and, response bias is mediated by a shift in a decision criterion. One can interpret the effect of attention as on either perception or decision. In summary, we account for spatial attention and response bias by a single model that predicts accuracy and response time.

[Supported by HHMI and NEI]

◆ **Selective attention as the substrate of optimal decision behaviour in environments with multiple stimuli**

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Making a decision is by essence an attentional state. We present a series of experiments originally intended to assess decisional behaviour in environments with multiple stimuli, and that eventually pointed to an intimate link between decision and attention. The experiments show that when subjects have to decide on the occurrence of one out of two concurrent (partial report) or sequential events, their decisional behaviour may depart from optimality (in the signal detection theory sense) in that it reveals the use of a ‘common denominator’ decision criterion. This ‘unique criterion’ (UC) is not observed when the two events are (a) within different modalities (an auditory intensity and a visual contrast increment) and (b) within the same modality (both visual or both auditory) but interfere. In the latter case, the occurrence of either of the two events can be more accurately detected by tagging it with the responses in the two interacting mechanisms, thus preserving the two-dimensionality of the stimulating condition. Stimuli invoking responses from independent mechanisms (within the same modality) require only one-dimensional tagging. On this view, the dimensionality of the tagging process matches that of the decision process. An equivalent way to phrase this is to say that the UC observed with non-interfering intramodal stimuli is the consequence of merging the decision axes associated with each of them. Classifying (physically distinct) events by means of keeping track of their characterising dimensions is a basic attentional process. Hence attention is, among others, a process by means of which decision axes (and thus response criteria) associated with each of the two (or more) concurrent or sequential events are kept apart. The merging of the decision axes may be conceptualised as the consequence of the ‘relaxation’ of attention. In short, the selective aspect of attention appears to apply to the dimensionality of decisions. The present audio – visual data suggest that sound pressure and luminance contrast cannot be merged within a unique dimension, even when these two dimensions do not interfere with each other.

ORAL PRESENTATIONS

LEARNING, MEMORY, DEVELOPMENT, AND AGEING

◆ **Episodic short-term memory for spatial frequency**

F Zhou, R Sekuler, M Kahana (Volen Center for Complex Systems, Brandeis University, MS 013, Waltham, MA 02454, USA; e-mail: fzhou@brandeis.edu; website: people.brandeis.edu/~sekuler/MemoryDemo)

Our objective was to determine if a series of visual stimuli is remembered as a single prototype or as distinct exemplars. On each trial of our experiment, participants saw a series of three briefly presented gratings, two study items followed by a probe item. Each grating comprised a vertical and a horizontal sinusoidal component; within a trial, the spatial frequency of the vertical component varied. Relying on memory of the vertical component of the study items, participants judged whether the probe was the same as one of the study items or differed from both. Individual discrimination thresholds of spatial frequency were used to scale the spatial frequency of the gratings. The spatial frequency of the stimuli tested recognition over a range of perceptual distances between probe and study items. The performance of participants was

summarised by 'mnemometric functions', which relate memory performance to inter-stimulus perceptual distance. With study items separated by 4 or 8 threshold units, the bimodality, shape, and peaks of the mnemometric functions indicate that study items were represented in memory as distinct, noisy exemplars that are centred on the spatial frequencies of the study items. The mnemometric functions were well fit by a three-parameter signal detection model, whose representation of the first study item was twice as noisy as the representation of the second study item. The model also shows that individual discrimination thresholds closely approximate decision criteria in episodic recognition, which represents a near-optimal rule for deciding whether a probe had been in a study set. The quantitative links between visual stimuli and memory performance demonstrate that multiple items are stored as noisy exemplars in episodic short-term memory.

[Supported by NIH grant 55687.]

◆ **Opposite effects of saccades on short-term and long-term visual memory**

J Ross, A Ma-Wyatt¶ (School of Psychology, University of Western Australia, 35 Stirling Highway, Nedlands, Perth, WA 6009, Australia; ¶ Smith-Kettlewell Eye Research Institute, 2318 Fillmore Street, San Francisco, CA 94115, USA; e-mail: jr@psy.uwa.edu.au)

Though some evidence suggests that very little visual memory remains after saccades, other evidence suggests what remains is substantial. Our aim was to investigate the effects of saccades on two forms of visual memory: memory for the states of bistable figures, and memory for stimulus contingencies. Bistable figures and a McCollough effect test pattern were observed under three conditions: continuous presentation (CP), intermittent presentation (IP), and IP with saccade (IPS). In the IPS condition, subjects made saccades away from the site of the stimulus when it disappeared and back to it when it reappeared. We found that bistable figures alternated less rapidly in the IP than in the CP condition, as recently reported (Leopold et al, 2002 *Nature Neuroscience* 5 605–609), but the rate of alternation increased in the IPS condition, in which observers made saccades. The McCollough effect persisted longer in the IP than in the CP condition. Persistence was greater still in the IPS condition. The results indicate saccades reduce the persistence of short-term visual memory for states of bistable figures. On the other hand they increase the persistence of long-term visual memory for stimulus contingencies, exemplified by the McCollough effect. Their effects on other forms of short-term and long-term memory are yet to be determined.

[Supported by Australian Research Council.]

◆ **Effects of visual and lexical factors on improvements in the recognition of flanked letters**

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Word recognition requires the identification of flanked letters. Recognition of flanked letters, however, is strongly impaired, especially in peripheral vision (so-called crowding or lateral masking phenomenon; eg Bouma, 1970 *Nature* 226 177–178; Huckauf et al, 1999 *Perception & Psychophysics* 61 177–189). Nevertheless, recognition performance for flanked letters can be enhanced by training (Huckauf, 2002 *Perception* 31 Supplement, 96). The first question at issue is how specific these improvements are. This was studied by presenting three-letter nonword strings in upper case at a certain eccentricity with a certain spacing between the characters. Before, during, and after training, recognition performance for the central target letter was assessed when varying the case, the eccentricity, or the spacing. Recognition performances increased with increasing training duration. After a short period of training, improvements were observed only for the trained condition. After a longer period of training, however, there was also a transfer to another case, location, and configuration of the string. Nevertheless, the superiority for the trained condition persisted, and the improvements as well as the superiority for the trained condition were obvious even 24 hours later. In a further experiment, it was tested whether training improvements depend on higher-level information of the strings. Although target letters were recognised better in orthographically legal relative to illegal strings, the improvements as well as the specificity of learning were comparable for both kinds of strings. These results will be examined further in another study with nonwords, words, and isolated letters used as comparison.

◆ **Influence of task demands on object representations**

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Visual working memory is often characterised in terms of information capacity, and measured as the number of integrated objects retained. However, the maximum number of 'object files' may

not be an appropriate measure of how visual memory is used during behaviour. Rather, we suggest that acquisition and retention of visual information is governed by task relevance. Subjects performed a sorting task in virtual reality with haptic feedback. Each trial required participants to select one of five bricks based on a particular feature (colour, width, height, or texture) and then to place it onto one of two conveyor belts on the basis of the same or a different feature. A change was made to one of the features of the brick being held on about 10% of trials and subjects were told to discard the brick into a 'waste bin' if they detected a change. Change detection was predicted by the relevance to the sorting task in addition to intrinsic salience of the different features. When only one feature was required for the task, subjects detected more changes to relevant features (36%) than irrelevant features (19%). When a second feature became relevant for sorting, change detection was greater for both the feature used for brick selection (46%) and the feature relevant for brick placement (42%) than for irrelevant features (26%). Pauses in hand movement during the sorting decision more frequently occurred following missed changes to relevant features than to irrelevant features. We conclude that immediate task demands govern the precise composition of visual working memory, the contents of which may be aggregates of task-relevant features.

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◆ **Plasticity, learning, and developmental processes contributing to 'dorsal vulnerability'**

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We have used sensitivity to global motion and form coherence in young and atypically developing children to compare extrastriate dorsal and ventral stream functions. Such studies indicate 'dorsal stream vulnerability' in a range of neurodevelopmental disorders (Atkinson et al, 1997 *NeuroReport* **8** 1919–1922; Gunn et al, 2002 *NeuroReport* **13** 843–847; Spencer et al, 2000 *NeuroReport* **11** 2765–2767). How far do differences in normal and anomalous development reflect differential attentional processes operating within the two systems? We have measured changes in sensitivity with repeated practice in the two tasks, in young adult subjects. Performance on global form coherence (detection of concentrically arranged line segments) showed relatively stable performance over time; whereas motion coherence thresholds (detection of segmented random-dot motion) showed significantly larger variations over repeated trials, both in initial learning and, in some subjects, later deterioration. These results suggest that our global-motion detection task is relatively more sensitive to attentional control processes, which are necessary to select and maintain specific strategies for information extraction. We consider the effect of this difference in sensitivity to practice effects in typical and atypical development, with data from 4–6-year-old children and individuals with Williams syndrome, and discuss current neurobiological models of these processes.

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◆ **Sensitivity to motion in the ageing visual system**

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The detection of movement is clearly vital in tasks such as driving, yet surprisingly little is known how this ability changes in the elderly visual system, or how any changes might be related to the more established changes associated with ageing (eg loss of spatial acuity). Previous studies that demonstrated a loss of motion acuity in the elderly all used stimuli that were broadband in nature; thus the loss may be associated with the loss of high spatial frequencies that could underpin the detection of very slow (or small) motions. We therefore measured motion acuity using both broadband and narrowband stimuli (gratings of spatial frequencies 0.5, 1, 2, and 4 cycles deg⁻¹) in a group of elderly observers and younger controls. In addition, we also examined visual acuity, and both spatial and temporal contrast sensitivity in these observers. Motion acuity was lower (approximately 3–5 dB) in the elderly observers for both the broadband and all the narrowband stimuli. This loss of motion acuity could not be accounted for by loss of spatial vision, as at the lowest spatial frequency tested the elderly observers did not show any loss in contrast sensitivity.

MULTISENSORY PERCEPTION

◆ Location-specific transfer from haptics to binocular vision

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The perceptual system efficiently combines haptic and visual information when perceiving 3-D form. At what levels of processing can this integration occur? And what strategies are used for binding the separate neural signals into a unified representation? Using random-dot stereograms (RDSs) whose perception was slowed by a carefully calibrated proportion of stereoscopic noise, we studied the influence of haptics on the time necessary to perceive disparity-defined forms. Participants blindly felt a bas-relief version of a square or a circle. After a fixed amount of time, the haptic surface was removed and vision was restored. A sparse RDS was then presented which contained a disparity-defined form that was either a square or a circle. These disparity-defined forms were presented either at the same location in peripersonal space as the felt surface or at a different location. Observers responded as soon as they could identify the shape with 100% confidence (as checked by analysing identification rates). Overall, response times clearly depended on whether the felt form was the same as the disparity-defined form. Average response times were equal to 14 s when seeing a circle after feeling a circle and to 15.7 s when seeing a square after feeling a square, but increased to 17.6 s and 21.8 s when seeing the circle and the square after feeling the other form. Moreover, this crossmodal transfer was virtually absent when the haptic surface was placed on a different plane or at a different position from that of the seen surface. These data suggest that haptics may interact with low-level processes involved in solving the correspondence problem for binocular vision, and that this process of crossmodal integration may be mediated by a common map of egocentric locations.

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◆ A common visual – auditory representation for eye and arm movement control?

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The question whether saccadic eye movements and goal-directed arm movements share control processes or are programmed separately is still unsolved. The effects of visual – auditory stimulation on eye and arm movements were analysed to clarify whether the respective motor control processes are based on the same multimodal representation. A common visual – auditory representation for movement-control processes may be assumed if experimental manipulations of a bimodal stimulus arrangement evoke analogous effects for both kinds of movement. In a focused-attention paradigm, subjects were asked to respond to a visual target stimulus with either a saccadic eye movement, a goal-directed hand movement, or both, and to ignore an accessory auditory stimulus. The effects of spatiotemporal visual – auditory stimulus relationship on movement latencies and error rates, found in the first experiment, contradict the notion of common control processes. In contrast, no evidence for separate movement programming with variation of auditory stimulus intensity was found in a second experiment. The conflicting results may be explained by the assumption that brain structures in charge of hand-movement control have the capability of a higher spatial resolution for auditory stimuli. A third experiment gives an indication of the origin of the higher spatial resolution and supports the notion of a common visual – auditory representation as a basis for eye and arm movement control.

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◆ Recalibration of temporal tuning of an audio – visual interaction by adaptation to a constant time lag

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Although temporal synchrony is a critical condition for the binding of visual and auditory events, time differences in physical and neural transmissions make it difficult for the brain to accurately judge the audio – visual simultaneity. One strategy our brain might take to overcome this difficulty is to adaptively recalibrate the point of simultaneity from daily experience of audio – visual events. This hypothesis is supported by a novel cross-modal adaptation effect we recently found (Fujisaki et al, 2003 *VSS03 Proceedings* 16). That is, adaptation to a fixed audio – visual temporal lag shifted the centre of the subjective simultaneity responses in the direction of the adapted lag. To test whether the lag adaptation also affects implicit, functional simultaneity, which could not be ascribed to a criterion change in cognitive decision-making, we examined post-adaptation

changes in the temporal tuning of the stream/ bounce illusion (Sekuler et al, 1997 *Nature* **385** 308), where a 'collision' sound presented near the crossover of two moving balls facilitates the perception of balls bouncing. To estimate the time span of this audio–visual interaction, which, we expect, reflects implicit simultaneity in the underlying neural hardware, we measured the frequency of bounce perception as a function of the audio–visual time lag, with and without adaptation to pairings of a tone and a collision made with a constant lag of, typically, –235 ms, 0 ms, or +235 ms. For five of the seven subjects we have tested, there was a significant shift of the centre position of the bouncing response towards the adapted lag. The results suggest that the lag adaptation can also recalibrate implicit judgments of audio–visual simultaneity, although the effect may not be as robust as that for the explicit simultaneity judgments.

◆ **The ventriloquist effect results from optimal cross-modal integration**

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Ventriloquism is the ancient art of making one's voice appear to come from elsewhere, usually explained by the conjecture that vision 'captures' sound. We investigate this effect by asking observers to localise spatially Gaussian light-blobs or sound-clicks, separately and presented together. In all conditions there were two brief presentations of stimuli, and observers were asked to indicate which of the two presentations appeared to be more rightward. For visual uni-modal presentations, localisation accuracy depended strongly on Gaussian width, being best (0.5 deg) for the smallest blobs and worst for the largest (12 deg). Localisation accuracy for the auditory click was around 6 deg, falling midway between the various visual stimuli. We next measured localisation for a blob and click presented together. On one presentation the stimuli were in conflict, with the visual stimulus displaced either side of the midline; on the other they were displaced together, left or right of midline. For small blob widths, localisation of the dual stimulus was dictated by the visual presentation, suggesting that vision dominated the perceived position of the incongruent stimuli (the ventriloquist effect), while for large blobs, the reverse held, with the click dominating perceived position (an 'inverse ventriloquist effect'). For the mid-size blobs both modalities contributed to the effect equally. The results are well explained by the Ernst and Banks (2002 *Nature* in press) model of statistically optimal combination of information across modalities, weighting each estimate inversely with the separately measured variance of that estimate.

◆ **Perception of visual illusions with a sensory substitution system**

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Experiments were undertaken to investigate the perception of different visual illusions with a prosthesis of substitution of vision by audition. Early blind and sighted blindfolded subjects were trained to use the prosthesis in a pattern recognition task before the study. The first experiment was designed to study the effect of various configurations of the vertical-bar illusion. The volunteers were asked to explore successively several stimuli projected on a computer screen and thereafter to decide whether the horizontal or the vertical bar appeared to be the longest. A separate experiment was then performed in a similar manner to test the Ponzo illusion, and the role of instructions leading, or not leading, to processing entirely each stimulus, especially the two converging oblique lines around the two horizontal ones. The results show that only sighted blindfolded subjects are affected by both visual illusions in a similar way as in normal vision. This highlights the importance of previous visual experience in the perception of visual illusions. It also appears that taking into account the context in which the illusion is induced plays a crucial role for perceiving the Ponzo illusion. In conclusion, these results suggest the existence of common processes governing the perception with substitution of vision by audition and the normal visual perception.

◆ **Cross-modal extinction in autism: A case report**

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Several first-hand accounts by people with autism describe strong cross-modal interference such that stimuli presented to one modality may become extinguished in the presence of stimuli from

another modality. One of these is TM, a 13-year old non-verbal low-functioning autistic, who is exceptionally capable of communicating through writing and performing complicated psychophysical tasks. TM occasionally complained that when he hears, his vision shuts down and vice versa. We investigated TM's cross-modal interference in a set of simple experiments that were performed by age-matched as well as younger controls without any difficulty. We used a briefly flashed (100 ms) rectangular (2 deg) high-contrast yellow patch on a black background and a short (100 ms) band noise (0–3 kHz). TM could easily detect both stimuli in isolation, but often failed to report the visual patch when presented simultaneously with the sound. Similar results were obtained with tactile stimuli, which were 'extinguished' by both visual and auditory stimuli. In another experiment, TM had to judge if the visual patch and the sound, which were presented in one of two sides (7° eccentricity) were presented in the same or different sides. TM failed to perform the task unless the visual patch was delayed by more than 1 s relative to the sound. Finally, TM failed in a dual report of colour (red/blue) and symbol (+/–) of a flashed visual pattern. This interference within modality did not occur between two symbols, or between motion and colour. We interpret the results in terms of 'extinction' between competitive mechanisms residing in different cortical modules that operate abnormally in a winner-takes-all fashion at different processing levels.

ACTION AND PERCEPTION, VECTION, OPTIC FLOW

◆ **Object-based attention and space-based attention depend on action intention**

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We investigated the impact of different motor demands on space-based and object-based attention allocation. Participants detected visual targets on object outlines that were shown on a touch screen, using Egly et al's paradigm (1994 *Journal of Experimental Psychology: General* **123** 161–177). Peripheral cues preceded the targets by 200 ms and were valid (same location as target, 67%), or invalid but on the same object (11%), or invalid and on the other object (11%), or catch trials (11%). Responses to targets were either lifting a finger, or pointing to the target, or grasping a clay object placed on the target location. Reaction times and movement times were recorded. Space-based attention is reflected in processing costs for invalid same-object trials over valid trials, and object-based attention is reflected in processing costs for invalid different-object trials over invalid same-object trials. Both dependent measures showed more space-based attention for pointing than for finger lifting and more object-based attention for grasping than for pointing. This result supports the view that visual selectivity is tuned to specific motor intentions (Bekkering and Neggers, 2002 *Psychological Science* **13** 370–374) and illustrates the tight coupling of perception and action. [Supported by British Academy (LRG31696).]

◆ **Saccades are sensitive to the Müller-Lyer illusion, pointing is not**

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We investigated visuomotor transformations involved in guiding saccades and pointing. Pointing and saccade accuracy were measured in response to a simplified Müller-Lyer illusion ('in' and 'out' arrows) and to a baseline condition ('+' pattern). Display time for all stimuli was 180 ms. Participants executed saccades or pointed from one arrow vertex to the other (or from the centre of a + to the other +). The starting point was always positioned at a central fixation point. The aim point was positioned randomly to the left or right of the starting point. In an additional pointing-after-pursuit task (Bruno and Bernardis, 2002 *Perception* **31** Supplement, 145), before pointing participants pursued the aim point as it moved away from the arrow or + at fixation. Finally, in a verbal-estimation task participants estimated the separation of the elements relative to a standard. There was a clear effect of the illusion on primary-saccade amplitudes. Relative to the baseline, average saccade amplitudes were reduced by $13\% \pm 1\%$ SE with 'in' arrows but increased by $9\% \pm 1\%$ with 'out' arrows. This pattern closely resembled verbal estimations (in = $12\% \pm 1\%$, out = $10\% \pm 3\%$). Conversely, there was essentially no effect on pointing amplitudes (in = $5\% \pm 2\%$, out = $1\% \pm 2\%$). These results confirm that saccades are sensitive to the Müller-Lyer illusion, but pointing is not. We conclude that neither efferent positional information from saccadic motor programs nor afferent information from fixations are necessary for guiding pointing movements and that oculomotor accuracy is tied to perceived positions and amplitudes. [Supported by Università di Trieste, and the Wellcome Trust.]

◆ **Colour vision and fast corrections to arm movements**

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There is an apparent discrepancy in the literature whether colour information can be processed quickly enough to guide our actions. Pisella et al (1998 *Experimental Brain Research* **121** 270–276) instructed subjects to point at green targets. When the target was displaced and simultaneously turned red, subjects pointed at the displaced target. The authors' conclusion was that it takes longer to process colour information than position information. However, we found that subjects react quickly to a change in position of a target differing only in colour from the background. The critical difference could be that, in their study, responses had to be selected on the basis of the judged colour, whereas in ours the colour itself was irrelevant because colour processing was only needed to determine the position of the target. To find out whether this difference was indeed critical, we asked subjects to move a pen across a digitising tablet. They had to move from a starting position to a red target. On some trials, the red target jumped as soon as they started moving towards it. We determined how various kinds of distractors influence the speed with which subjects respond to such jumps. The distractors differed in the extent to which they made it necessary to analyse the colour for choosing a response. Subjects took longer to respond whenever they had to use colour to distinguish the target from the distractors. We conclude that it is the selection process rather than colour processing per se that takes more time.

◆ **Critical sensorial information for a goalkeeper engaged in penalty**

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Cognitive sport psychology is an emerging reality in the domain of experimental human sciences for a better understanding of how athletes develop mental strategies to optimise their performance. This aim can be achieved, for instance, by using the paradigms of visual sciences in analysing the sensorial cues available to an athlete performing a specific motor task. In soccer, a typical motor action is that of the goalkeeper trying to save a penalty shot. Video-recording of a large number of penalty kicks from the goalkeeper's point of view can be used to set up a video-test and a video-training to be proposed to the goalkeeper. The aim of the present work was to investigate which are the relevant visual cues informing the goalkeeper about the final direction and the speed of the ball. We asked several semi-professional soccer players to take a large number of penalties. They were requested to shoot for goal to eight different locations. All the penalties were video-recorded from the goalkeeper's perspective. Video-training was based on the systematic manipulation of the visual information coming from different parts of the shooter's body. We found that it is possible to manage relevant visual cues to make the goalkeeper improve her/his performance by using visual search mental strategies to activate the right motor reactions.

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◆ **Visual perception of a single plane during sagittal head motion**

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During head translations along the sagittal axis, a stationary plane slanting in depth is perceived as rotating in depth. This perceived concomitant rotation (PCR) is synchronised with head translations, and absent for lateral translations. We questioned whether it is related to the twofold ambiguity predicted for the recovery of plane orientation from motion (Longuet-Higgins, 1984 *Proceedings of the Royal Society of London, Series B, Biological Sciences* **223** 165–175). Subjects moved their heads backward and forward, viewing computer-generated stimuli representing dotted planes. The slant (angle between the stimulus plane and the frontal plane) was 30° or 45°, with a horizontal tilt; the simulated viewing distance was 70 cm or 140 cm; the field of view was 30° or 60°. With a headtracker, the eye position in space was recorded to generate motion parallax in the display. The plane rotated in depth in synchrony with the head movements. The subject adjusted the rotation magnitude, so as to restore a maximal apparent stationarity. As predicted by Longuet-Higgins, the PCR axis is orthogonal to the plane tilt (direction of maximal slope). Its magnitude reverses with the tilt direction, and increases with slant. It is only a fraction of the spurious solution obtained by Longuet-Higgins. The PCR occurs for a single plane, and disappears for multiple-facet objects. It is higher for object motion, as compared to self-motion. We conclude that Longuet-Higgins's theory partly accounts for the PCR of a plane during sagittal motion. The percept is intermediate between the true and spurious solutions.

The PCR is smaller for self-motion, as compared to object motion, supporting a partial integration of self-motion information in the visual processing of optic flow.

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◆ **Context-based structuring action on optic-flow fields by generative models of first-order motion primitives: Velocity likelihoods and Gestalt detection**

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The problem of providing evidence for the presence of a certain complex feature in the optic flow can be posed as an adaptive filtering problem, where local information acts as the input measurements and the context acts as the reference signal, eg representing a specific motion Gestalt. In this context, we defined a set of context-sensitive filters (CSFs) built on opponent and non-opponent elementary gradient-type velocity patterns (Treue and Andersen, 1996 *Visual Neuroscience* **13** 797–804), as cardinal components of a linear deformation space (Koenderink, 1986 *Vision Research* **26** 161–179). By checking for the presence of such Gestalts in optic-flow fields, we make the interpretation of visual motion with more confidence, by assigning the most probable pattern to a group of velocity vectors, on the basis of their spatial relationships. Casting the problem as a Kalman filter, the detection occurs through a spatial recurrent process that checks the consistency between the spatial structural properties of the input-flow-field pattern and a structural rule expressed by the model equation of the Kalman filter. The resulting CSF behaves as a template model. Yet, its specificity lies in the fact that the template character is not built by highly specific feedforward connections, but emerges through stereotype recurrent interactions. We think that the approach can be extended to adaptive cross-modal templates (eg motion and stereo). By proper specification of the transition matrix in the model equation of the Kalman filter, it can, indeed, potentially model any type of multimodal spatiotemporal relationship (ie multimodal spatiotemporal context).

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BINOCULAR VISION, DEPTH, STEREO AND SPACE PERCEPTION

◆ **Perception and misperception of carved and developable textured surfaces**

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When a patterned sheet is folded into a developable shape, the pattern on the surface remains unchanged, but if the same shape is carved from a solid whose parallel planes are identically patterned, the pattern on the surface is distorted as a function of the shape. 3-D-shape extraction can thus assume that texture distortions in retinal images are solely due to projection for developable surfaces, but not for carved surfaces. We compared the perception of sinusoidally corrugated developable and carved surfaces, and generalised the results to non-developable, carved, doubly-curved, sinusoidal depth-plaids. To identify neural mechanisms of shape perception, we analysed perspective images in terms of orientation and frequency modulations. Veridical 3-D-shape perceptions for both classes require the visibility of signature orientation modulations arising from similar Fourier components of the texture pattern. Frequency modulations in perspective images of developable surfaces arise from changes in surface depth and slant, but for carved surfaces they arise almost entirely from changes in depth and thus are greatly reduced. Concavities and convexities of developable surfaces with isotropic textures are often perceptually confused owing to similar slant-caused frequency modulations, but these confusions do not occur for carved surfaces. For depth plaids, veridical percepts of concavities, convexities, and saddles require the visibility of critical orientation modulations around each of the two axes of depth modulation. However, in isolation, doubly-curved concavities often appear convex or flat. Despite differences in surface texture mapping between developable and carved surfaces, 3-D-shape percepts rely on similar orientation modulations, and similar neural mechanisms.

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◆ **Emergence of motion-in-depth selectivity in the visual cortex: An evidence of phase-based second-order motion mechanisms?**

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The question which mechanisms are responsible for second-order motion perception has an important bearing on the issue whether the brain adopts a specialised second-order (non-Fourier)

motion channel or relies upon the hierarchical combination of the motion signals conveyed by the first-order (Fourier) channel (Chubb and Sperling, 1988 *Journal of the Optical Society of America A* **5** 1986–2006). We propose and analyse a type of second-order motion computation in which motion energy mechanism is applied to a population of disparity-tuned units (compare V1 cells—Ohzawa et al, 1997 *Journal of Neurophysiology* **77** 2879–2909) to compute motion toward/away-from the observer. We demonstrate that binocular energy complex cells relay phase temporal derivative components that can be combined, at a higher level, to yield a specific motion-in-depth (MID) selectivity. The rationale of this statement relies upon analytical considerations of phase-based dynamic stereopsis, as a time extension of the well-known phase-based techniques for disparity estimation (Fleet et al, 1991 *Computer Vision, Graphics and Image Processing: Image Understanding* **53** 198–210). On this basis, an architectural cortical model for MID selectivity in the visual cortex is proposed. By hierarchical combinations of the same signals provided by spatiotemporal frequency channels, the resulting cortical units actively eliminate sensitivity to a selected set of parameters, thus becoming specifically tuned to different features, such as disparity but not MID, or MID but not disparity. The emergence of MID tuning is discussed in relation to unbalanced ocular dominance of afferent binocular contributions. [Supported by the CEC IST-FET Project 2001-32114 'Ecovision']

◆ **Perceived depth during head and eye rotation**

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Objects translating in the frontoparallel plane give rise to patterns of retinal motion that can serve as local cues to depth. Accurate tracking by eye and head alter these cues by cancelling retinal translation, leaving relative motion alone (eg shear). On its own, relative motion has ambiguous depth sign (as in the kinetic depth effect) which becomes unambiguous during eye or head movement. This suggests extraretinal signals are used to interpret motion cues to depth. Local depth change is proportional to the ratio of relative motion to translation ($D \sim S/T$). Perceived depth should therefore increase during pursuit, because eye movement perceptually slows moving objects. We investigated this hypothesis and extended the analysis to head rotation. We determined psychometric functions for perceived speed and perceived depth of sine-wave corrugations. A 2IFC technique was used in which the translation in eye-and-head-stationary intervals (T_s) was varied while keeping constant the translation in eye-moving or head-moving intervals ($T_m = 4, 6, \text{ or } 8 \text{ deg s}^{-1}$). Relative motion (cosinusoidal shear, spatial frequency = $0.1 \text{ cycle deg}^{-1}$, amplitude = 0.1 deg) was constant in both intervals. At the match-point, we found that eye-tracked and head-tracked stimuli appeared half as slow as eye-and-head-stationary stimuli (T_s/T_m , head = 0.53, eye = 0.53, three observers). However, the same was not true when judging perceived depth (T_s/T_m , head = 0.17, eye = 0.16), suggesting a strong influence of retinal translation in the recovery of shear. By factoring out changes in perceived speed, we find that retinal translation lowers the visual estimate of shear by about 3 times in the conditions tested. [Supported by EPSRC.]

◆ **Disentangling retinal and head-centric disparity-coding involved in perception of metric depth from stereo**

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Recovering metric shape-in-depth from azimuthal disparities between retinal images requires a transformation which depends on the viewing distance. Does this transformation act on a retinal disparity field, or is it preceded by a transformation of retinal images to head-centric disparities (Erkelens and van Ee, 1998 *Vision Research* **38** 2999–3018)? Earlier work (Domini et al, 2001 *Vision Research* **41** 2733–2739) found little if any role for 'raw' retinal disparity field curvature in the representation of shape in depth, but this does not answer our question. To disentangle retinal and head-centric disparity processing, subjects 'nulled' the perceived curvature of a cylindrical (or spherical) test-patch, after adapting to a convex or concave patch for a variety of conditions – being mainly combinations of (A) either fixating on the stimulus-centre, or tracking a figure-8 path in version and vergence, to smear out the local retinal disparity and its gradient; and (B) showing the adaptation and test stimuli either in the same or the opposite head-centric hemifields. About $\frac{3}{4}$ or more of the curvature adaptation survives even combined retinal disparity smearing and transfer to the opposite head-centric hemifield. The effects of factors A and B apart, and their interaction, are small: up to about 10%, if at all significant. The transfer across

head-centric hemifields indicates that metric shape-in-depth is not computed from a head-centric representation. The near-absent effect of smearing the retinal disparity by version and vergence scanning, combined with the weak (if any) transfer between opposite retino-centric hemifields (control) suggests a model in which metric curvature in depth is computed 'early', by neurons that encode the curvature of the retinal disparity field, but combine it directly with a vergence signal. [AJN and AvdB are supported by HFSP grant RG 0071/2000-B204.]

◆ **A robust and optimal model of cue integration**

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Ernst and Banks (2002 *Nature* **415** 429–433) provided evidence that the brain integrates haptic and stereo cues in a statistically optimal way—the weights given to each cue when presented together were proportional to the reliabilities obtained for each cue alone. Other recent experiments have also supported this result. However, there are everyday examples that seem at odds with this view. For example, our ability to see depthful scenes depicted on television or cinema screens, or monitors used in psychophysics experiments, suggests that sometimes very reliable cues, such as stereo, can be ignored or vetoed. The visual system therefore also appears to be statistically robust in the sense that it can ignore a reliable cue if it conflicts with other cues. This is true even if these other cues are less reliable but are perhaps given greater weight because together they are in close agreement. The maximum likelihood estimation method used by Ernst and Banks does not provide a good framework for modelling such types of cue integration. We present an alternative model that is both robust and optimal. This model is similar in principle to the robust ideal-observer model (Porrill et al, 1999 *Nature* **397** 63–66). We describe an experiment designed to test the integration of conflicting and consistent stereo and texture cues from stereograms of a set of parabolic ridges shown at a range of orientations. The dependent variable was perceived ridge amplitude. We show how this model can account for the data obtained if blur cues to the flatness of the monitor are incorporated. The model also provides a natural way of accounting for individual differences within the data set.

◆ **A neurally based computational theory of binocular combination**

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When the left and right eyes view similar but slightly different stimuli, how are they combined to form the perceived 'cyclopean' image? To obtain the basic data for such a theory, observers viewed parallel, horizontal sine-wave gratings that differed in phase and in contrast between the two eyes. The sum of two such sines is itself a sine. The phase of the perceived sine is used to compute the relative contribution of each eye to the cyclopean image. Our neurally based gain-control model proposes that each eye not only inhibits the other eye in proportion to its own contrast energy, but also inhibits the other eye's reciprocal inhibition. The cyclopean image is the sum of the surviving signals from the two eyes. This theory has the robust (and correct) property that, when the two eyes have identical inputs, the cyclopean image is the same as when one eye alone receives input. It also makes excellent predictions of all the cases in which the images in the two eyes differ in relative phase and in contrast. It makes the prediction, which was verified, that adding random noise to the sine-wave in one eye will increase its relative contribution because the more-stimulated eye then exerts more gain control over its competitor. The gain-controlling property of added band-limited noise is used to determine the bandwidth of the competitive gain-control mechanism. The elaborated theory makes pixel-by-pixel predictions of the content of the cyclopean image, and accounts for the results of many classical experiments in binocular combination.

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WEDNESDAY
INVITED SYMPOSIUM 3**MULTISENSORY AND SENSORIMOTOR INTERACTIONS**◆ **Multisensory processing and plasticity in the superior colliculus**

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Combining information across different sensory modalities can improve our ability to detect, localise, and identify stimuli, and results in faster reaction times following stimulus presentation. Although many different brain regions receive converging sensory inputs, electrophysiological studies of the superior colliculus have been at the forefront of our attempts to reveal the cellular principles underlying multisensory integration and plasticity. This midbrain nucleus transforms visual, auditory, or tactile signals into motor commands that control orienting behaviour. The registration of these maps provides a framework for behaviourally significant interactions to take place between different sensory inputs. The emergence of map registration during development, which takes place against a background of growth-related changes in the relative geometry of the different sense organs, is an activity-dependent process. In particular, the neural circuits underlying the auditory representation are shaped by experience. Studies in ferrets and owls have revealed that visual signals arising from the superficial layers of the superior colliculus guide the maturation of the auditory spatial tuning, thereby ensuring that intersensory map alignment is achieved. In this talk I consider how the neural circuits underlying the auditory representation are shaped by experience, as well as the crossmodal consequences of a loss of vision during early life.

[Supported by the Wellcome Trust.]

◆ **fMRI studies of action and perception pathways in an individual with visual form agnosia**

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Ten years ago, Goodale and Milner proposed that visual information is processed differently for the control of actions than it is for constructing our perception of the world. Vision-for-action, they argued, is mediated by mechanisms in the dorsal stream, whereas vision-for-perception is mediated by mechanisms in the ventral stream. Some of the most compelling evidence for this distinction came from studies of DF, an individual with visual form agnosia, who is able to use vision to adjust the posture of her hand to the size, shape, and orientation of a goal object as she reaches out to pick it up—even though she shows no perceptual awareness of these same object attributes. New anatomical MR studies show that ventral-stream areas implicated in object recognition are severely damaged in DF. Complementary fMRI experiments revealed no differential activation in these or other areas of DF's ventral stream when she was presented with line drawings of common or novel objects (versus scrambled versions of these objects). In contrast, when DF reached out to grasp objects of different sizes and orientations, she showed relatively normal activation in dorsal-stream areas implicated in the visual control of grasping. These findings provide additional support for the proposal that vision-for-perception and vision-for-action depend on quite separate visual pathways in the cerebral cortex.

[Supported by Canadian Institutes of Health Research.]

◆ **Cross-modal synergies in spatial attention**

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Although selective attention has traditionally been studied for one sensory modality at a time, numerous psychophysical or reaction-time experiments have now shown cross-modal spatial synergies. Attention to a particular location for one modality can influence processing for that location versus elsewhere in other modalities also. We briefly review psychological findings of this type, before turning to ERP and fMRI studies on their neural basis. We find that cross-modal attention effects can influence brain areas and components that would usually be considered 'unimodal' (eg attention to a particular location in touch can modulate neural responses to visual stimuli from that location, in occipital cortex). Such effects may involve feedback influences from supramodal control processes for spatial attention in parietal and frontal cortex.

[Supported by the MRC (UK).]

◆ **Plasticity of visual functions: The case of deafness and video-game playing**

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To what extent can visual functions be modified by altered experience? I first address this question by considering the impact of deafness on vision. Current findings indicate that deaf individuals do not have 'better' vision, but do have specific enhancements in some aspects of visual attention. This research supports the existence of compensatory cross-modal plasticity, but suggests it is limited to a small set of attentional skills and most likely mediated by cortical changes in higher-level visual centres such as the parietal cortex. Second, by studying the impact of video-game playing on vision, it has been observed that a number of visual skills that are not modified by deafness can be effectively changed by video-game training. Thus, the specificity of the changes induced by deafness cannot be explained by a mere lack of plasticity in these visual functions. Rather, the research reported here highlights the pivotal role of experience in shaping visual skills.

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◆ **Cognitive strategies, decision, and changes in point of view in multisensory perception: The example of navigation**

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During navigation, the brain can use several cognitive strategies to memorise a travelled path: (a) it can use a 'route', egocentric, strategy which includes memory of kinaesthetic information (body movements) and associations between visual landmarks or events and movement; (b) it can also use a survey, allocentric, strategy using a mental visual map of the environment. This second strategy allows shortcuts or detours. Most existing models of multisensory integration during navigation suppose that, when a conflict occurs between the different sensory modalities, the brain can solve the coherence problems by weighing the values of the different sensory channels. This 'weighing' method is not the only one possible. I propose a new theory of conflict solving and hypothesise that the brain makes a decision and selects one modality, or a small combination of sensory inputs depending on the context and the task. This top-down decision process is suggested by experiment in which a conflict was created during a navigation in a virtual-reality labyrinth in association with body movements. Manipulation of the respective gains between visual and kinaesthetic cues allows the measurement of the memorised travelled path. In addition, navigation in a virtual town makes it possible to study the brain mechanisms associated with memory of landmarks and route. I suggest that there is a dissociation between the right and left brain in the coding of visuo-spatial versus categorical and sequential aspects of the perceived environment. Finally, fMRI data allow the identification of brain structures involved in the changes in the point of view necessary for elaborating the adequate cognitive strategy.

◆ **Connecting vision with the world**

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I have previously argued (Pylyshyn, 2001 *Cognition* **80** 127–158) that there are both logical and empirical reasons for postulating a certain kind of non-semantic or non-conceptual connection between parts of visual representations and distal visual elements. This sort of connection can be viewed as a pointer or deictic reference (Ballard et al, 1997 *Behavioral and Brain Sciences* **20** 723–767). I describe several experiments that illustrate the function of such mechanisms (which we have referred to as FINSTs). I also present several arguments why there must be something like a deictic pointer in order to 'situate' visual representations and connect them with their referents in a way that makes incremental construction of representations as well as visuo-motor coordination possible. To make this point concrete, I describe a series of experiments, focusing on the multiple object tracking paradigm, that reveal a variety of properties of this deictic reference mechanism. I also briefly allude to the implications of the FINST mechanism for a wide range of problems concerned with vision and with the foundations of cognitive science.

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INVITED SYMPOSIUM 4

NEUROPSYCHOLOGY OF VISUAL EXTINCTION

◆ Natural extinction

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Visual extinction is defined as the reduction in the frequency of “seen” reports to a stimulus when shown in the presence of another stimulus. Extinction effects are not limited to abnormal brain functioning. In binocular rivalry, two stimuli compete for awareness, and the more salient one wins. In the recently discovered motion-induced blindness, a salient stimulus may lose access to awareness in the presence of a moving-dot pattern presented to the same eye(s). This can be explained by assuming inhibitory processes acting between attentional (or recognition) modules responding to the different visual patterns. Extinction can also occur when the brain fails to match the different stimuli encountered with a coherent internal representation. Signal detection theory (SDT) offers a formal method to handle such a situation. According to SDT, the observer sets a criterion level of visibility based on likelihood estimates derived from the internal distributions of the responses evoked by the stimuli. We examined the process of criterion setting by presenting observers with two targets requiring their independent detection; an efficient detection strategy requires two separate internal representations, one for each stimulus. We found that the detection criteria set by the observers converged, as if based on a unified internal representation. For targets of different sensitivities, either due to stimulus parameters or to retinal non-homogeneity (left/right, up/down), the results showed higher criteria for the target with lower d' and lower criteria for the target with the higher d' (only when presented simultaneously or in temporal proximity), without a change in d' . Thus the frequency of “seen” reports for the less salient target was significantly reduced in the presence of the more salient target—an extinction effect. We have recently confirmed this behaviour for the appearance of highly suprathreshold stimuli.

◆ Neural correlates of visual processing with and without awareness in patients with extinction

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Visual extinction entails a loss of awareness for stimuli contralateral to a focal brain lesion (most often in the right parietal lobe) when competing stimuli are simultaneously presented in the ipsilesional field. Behavioural studies have suggested that extinguished stimuli may still be processed without attention or even without awareness. In keeping with such findings, I present results from event-related fMRI and evoked-potential studies on patients with neglect and extinction, indicating that unseen visual stimuli can still activate areas in the ventral temporal cortex. By contrast, awareness appears to be associated with greater activity in a distributed network of areas, at both early and later stages of visual processing, particularly in parietal and frontal areas. Retinotopic mapping of visual cortex spared after focal parietal damage also shows a modulation of fMRI responses in early cortical areas of the damaged hemisphere, not only affecting V1, but progressively increasing along the ventral visual pathways towards higher areas, such as V4 and beyond. These results suggest that residual processing in extinction may occur predominantly at relatively early stages of visual analysis, but may fail to reach higher stages and to be integrated with concomitant processing in dorsal stream without awareness.

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◆ Temporal dynamics of extinction

C Rorden (School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK; e-mail: chris.rorden@nottingham.ac.uk)

Extinction is typically measured with the ‘double simultaneous stimulation’ task, where two items are presented at the same moment. In this task, patients only report the ipsilesional item, despite the fact that they can accurately report a single item presented at any location. Implicit to this technique is the idea that the worst performance occurs when the stimuli are objectively simultaneous. Here I review a number of studies that have attempted to measure the temporal dynamics of extinction. Most of these studies suggest that patients do indeed show maximal extinction when information is objectively simultaneous, with reduced extinction as the delay between onsets increases. In contrast, a few experiments suggest that maximal extinction occurs when the ipsilesional item is presented slightly before the contralesional item. This discrepancy may be due to individual differences between patients, or it may reflect differences in the experimental

designs. I try to resolve these different findings, arguing that patients use top-down control to modulate their deficit, leading to different patterns of behaviour in different situations. This work can give us insight into this neurological condition as well as a refined understanding of the intact brain.

◆ **Perception, place, and identity. Is extinction a lack of a 'where-ness' for objects?**

G C Baylis, L L Baylis, C Rorden (University of South Carolina, Columbia, SC 29208, USA; e-mail: gordon@sc.edu)

Extinction appears at first to be a paradoxical phenomenon, since patients fail to notice stimuli in the 'bad' perceptual field opposite a lesion only when a stimulus is also presented to the 'good' field. For almost a century, this was explained purely descriptively as one stimulus 'extinguishing' the other. More recently, studies from our group and others (eg, Veuillemier, Rafal) have deepened the paradox by showing that the extinguished stimulus is largely processed by the patients' brains even when they do not report it. We have noted that visual extinction often results from lesions that disconnect visuo-spatial areas of the brain from areas that process visual identity. This has led to the suggestion that extinction may be caused, at least in part, by a failure to conjoin the identity of an item to its location, and that awareness of objects entails such a conjunction. Thus, for patients with extinction, despite the fact that their brain processes the identity of an item and its location, no conjunction leads to a lower probability that the patient will be aware of that item. Data from visual, auditory, and tactile extinction are discussed that support such a view, and explain the necessity of items in the 'good' field to elicit extinction.

◆ **The role of action in space perception**

M J Riddoch, G W Humphreys (School of Psychology, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK; e-mail: M.J.Riddoch@bham.ac.uk)

Previous studies have demonstrated that selection for perceptual report is often limited to one object at a time, with elements being selected together if they belong to part of the same perceptual group. Here, we use the neuropsychological phenomenon of extinction in patients with parietal lesions to show that selection is influenced also by action relations between objects. Performance is better when objects are positioned spatially so that they can be used together, relative to when the positions of the objects are inappropriate for their combined use. The action relation appears critical, since performance for pictures is not improved if the items are verbally associated. The opposite result occurs with words. Co-positioning objects for action 'glues' them together for visual selection, the effects emerging even on trials where only one object can be reported. The effects of verbal associations may, instead, reflect priming between lexical entries. Action relations between objects are not only important for visual selection, they can also influence the binding of objects to space as we demonstrate in a patient with Bálint's syndrome. Perception-action couplings appear to be critical for the conscious representation of space.

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◆ **Selective attention for identification model (SAIM): Computational modelling of visual extinction and neglect**

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Recently, we have presented a computational model of human visual attention, termed SAIM (selective attention for identification model), based on the idea that there is competition between objects for recognition (Heinke and Humphreys, 2003 *Psychological Review* **110** 29–87). SAIM uses a spatial window to select visual information for object recognition, ensuring both that parts are bound correctly within objects and that translation-invariant object recognition can be achieved. We showed how such a competitive model can provide a qualitative account of a range of psychological phenomena on normal and disordered attention. In this paper, we report a series of simulation results on extinction and neglect and discuss their implications for theories of attention. With these simulation results, SAIM can unify 'attentional' and 'representational' accounts of extinction and neglect, since a lesion can prevent all parts of stimuli from being attended, and it can disrupt the formation of translation-invariant representations of stimuli. In addition, SAIM is capable of simulating a classical deficit of neglect patients in the spatial-cueing paradigm (Posner et al, 1984 *Journal of Neuroscience* **4** 1863–1874). For SAIM, the deficit appears owing to an imbalance in the spatial-selection process rather than the impairment of a disengagement process as has often been suggested. Interestingly, this imbalance can also explain evidence on displacements of the location where the cue is most effective in neglect patients, as found by Pavlovskaya et al (1997 *Journal of Cognitive Neuroscience* **9** 824–834).

ORAL PRESENTATIONS

MOTION—LOW LEVEL

◆ When S cones contribute to global motion processing

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At last year's ECVF (Ruppertsberg et al, 2002 *Perception* **31** Supplement, 83) we presented evidence that global motion extraction for isoluminant stimuli is mediated by a red–green opponent (L–M) mechanism and found little evidence for S-cone input to global motion. It is reasonable to expect that scale is a critical factor in comparing colour mechanisms as cone spacing varies. We have now further investigated the conditions under which S cones contribute to the extraction of coherent motion. We measured motion discrimination thresholds (81%) as a function of chromatic contrast along an isoluminant yellowish-violet colour direction. Along this colour direction only the S-cone contrast is varied (Derrington et al, 1984 *Journal of Physiology* **357** 241–265). We used random-dot kinematograms with 150 coloured Gaussian blobs. In a 2IFC task observers had to distinguish between random motion and 40% coherent motion. Thresholds were assessed for different blob sizes (0.22 deg and 0.86 deg) and different displacements (0.233 deg and 1.165 deg). To exclude the possibility that a residual luminance component is used for the extraction of motion, we added luminance noise to the chromatic stimulus. We found that human observers are able to reliably discriminate between random and coherent motion for S-cone stimuli when the individual blobs are sufficiently large (0.86 deg) and displaced by a large amount (1.165 deg). We conclude that S-cone input to global motion processing is only effective for relatively large displacements (> 1 deg) and large stimulus sizes (≥ 1 deg). The required displacement is much larger than the S-cone spacing.

[Supported by the Wellcome Trust.]

◆ Contrast dependence of centre–surround interactions in motion processing: A MAE study

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We have recently demonstrated that increasing the size of a high-contrast moving object can make its motion more difficult to perceive [Tadin et al, 2003 *Nature* (in press)]. This counterintuitive finding is consistent with the involvement of motion-sensitive neurons with centre–surround receptive fields, such as those found in visual area MT. Surround inhibition is characterised by a decrease in neural activity in response to a large moving stimulus. This decreased activity may be evident in weaker adaptation of centre–surround neurons during prolonged exposure to large-field motion. As adaptation is associated with the motion aftereffect (MAE), we hypothesised that adapting to a large high-contrast moving stimulus should result in a weaker MAE. We explored this prediction by inducing MAE with moving Gabor patches of various sizes and contrasts and testing for MAE with a small test stimulus. As predicted, MAE strength decreased with increasing size when observers adapted to a high-contrast Gabor patch, suggesting spatial suppression. On the other hand, when a low-contrast adapting stimulus was used, MAE strength increased with increasing size, indicating spatial summation. These results support the notion that neurons involved in perceiving motion direction are inhibited when stimulated with a large high-contrast moving stimulus. Contrast dependence of this result indicates that spatial properties of motion perception are dynamic and stimulus-dependent. Thus, the visual system processes motion efficiently and adaptively by employing computationally advantageous inhibitory mechanisms only when the sensory input is sufficiently strong to ensure visibility.

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◆ Complementary computations for motion binding, segregation, and the neural solution to the aperture problem

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Motion can be locally measured by neurons orthogonal to an extended contrast (aperture problem), while that ambiguity disappears for local features (junctions). Combining several local measures of a moving form reveals the velocity of the object. Cortical mechanisms provide a dynamic solution to the aperture problem: MT cells initially represent normal flow, orthogonal to local contrasts, but after 150 ms the responses shift to encode the true stimulus direction (Pack and Born, 2001 *Nature* **409** 1040–1042). We propose a recurrent computational model of V1–MT integrating V1 motion signals along the feedforward path by MT cells (RF ratio 1 : 5). Divisive inhibition of ambiguous motion signals leads to flat population responses, whereas unambiguous

signals generate increased and sharply tuned activities. Modulatory feedback in turn emphasises V1 activities of matching velocity and suppresses incompatible measures (filling-in of unambiguous signals). Psychophysical investigations suggest features to be integrated only when they are intrinsic to a moving boundary, whereas extrinsic signals should be suppressed (Shimojo et al, 1989 *Vision Research* **29** 619–626). We suggest interactions with the ventral form path to unbind motion signals at occluding (extrinsic) boundaries. Simulations of moving bar sequences show spatially restricted MT-cell responses, which initially signal normal flow and then gradually switch to the true velocity by filling-in motion interpretations from (intrinsic) line endings. Our model predicts disambiguated motion responses also at the stage of V1 (feedback). The time course of switching neuronal responses depends on the length of stimulus bars. Further, motion and form path interactions help to robustly and selectively control motion binding and segregation of partly occluded patterns.

◆ **Barber poles and MT cells**

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Local measurements of visual motion are ambiguous along extended contours, but unambiguous at contour endpoints ('terminators'). When contour and terminator signals are pitted against each other with, for example, 'barber-pole' stimuli, terminator motion dictates perception. We have used such stimuli to measure direction-tuning curves of neurons in area MT of alert monkeys to ask if, and to what extent, terminator motion is favoured by early direction-selective cells. We found that sustained directional responses were dominated by terminator signals, being very close to those predicted by a vector-average of terminator signals only. The earliest directional responses, however, reflected predominantly contour motion with a gradual evolution, over ~100 ms, to the final terminator-dominated representation. The ultimate emphasis on terminator motion was unaffected by changes in size of the barber poles or by changes in their location within the receptive fields of the neurons. In a second series of experiments, we pitted extrinsic against intrinsic terminators by flanking square-aperture gratings with pairs of vertical or horizontal occluders. This had the effect of reducing the influence of the extrinsic terminators on MT responses to about half that of the intrinsic terminators. We conclude that MT neurons ultimately give much greater weight to terminator-based than to contour-based motion signals and to intrinsic over extrinsic terminators. This emphasis on terminator motion may result from an earlier stage of visual processing in which V1 neurons are rendered less sensitive to contours through end-stopping.

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◆ **Averaging of motion across short-interval displacements**

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Apparent motion enables us to see motion in movies and on electronic displays such as televisions and computer monitors. The alleged explanation for apparent motion is that neurons early in the visual cortex act as spatiotemporal filters that smooth out discrete displacements, rendering apparent motion indistinguishable from natural motion. Recently, I presented a novel apparent-motion stimulus showing that, at temporal frequencies higher than 30 Hz, human observers perceive motion in directions opposite to those predicted by spatiotemporal filtering (Erkelens, 2002 *Journal of Vision* **2** 705a). To clarify the counterintuitive observation I measured motion detection in response to short-interval displacements in two-frame and three-frame kinematograms (random-dot patterns of 36 deg × 36 deg), in which displacement (up to 18 min of arc) and SOA (between 13 and 52 ms) were the independent variables. The results show that motion detection thresholds are related to stimulus velocities (ratios of displacement and SOA), averaged across direction and across time within a window of about 40 ms. Temporal and directional averaging explains the motion perceived at high temporal frequencies. These properties of motion detection are incompatible with those of cortical motion-selective cells reported in the literature. The hypothesis is put forward that high-frequency detection of motion results from a low-level process, which may already start in the eyes.

◆ **Two motion aftereffects from a single coherent moving stimulus**

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After prolonged viewing of motion in one direction, a posterior stationary stimulus is perceived as moving in the opposite direction. This phenomenon is known as a motion aftereffect (MAE)

and can be obtained for both translational and more complex (eg rotational) motions. Verstraten et al (1998 *Perception* **27** 1055–1066) showed that the slow-velocity and fast-velocity components of a transparent motion could induce independent MAEs. The MAE had the opposite direction to that of the slow component when a static test stimulus was used, but it was perceived opposite to the fast component when tested with a dynamic stimulus. In their experiment, the slow and fast components were conveyed by independent parts of the stimulus during the adaptation phase. Thus their subjects could effortlessly perceive the two directions of motion within the adaptation phase. The optic flow that we are exposed to in daily life often also consists of different components, but these are perceived as a single coherent motion. In this experiment, we show that it is possible to decompose slow and fast motion components while having such an integrated percept in the adaptation phase. Subjects adapted to a spiral-like rotating stimulus. With a static test stimulus, an expansion (or contraction) MAE was perceived, which corresponded with the opposite direction of the underlying slow component of the adaptation stimulus. With a dynamic test, a rotational MAE was observed, which corresponded with the opposite direction of the fast-velocity component.

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◆ **How to make motion parallax stimuli by using an inverse Fourier transform**

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Motion parallax is a difference in image velocity that is due to a difference in depth. One interesting example of motion parallax is the motion of falling snowflakes during a snowfall. Snowflakes that are close to the observer fall with a greater image velocity than snowflakes that are far from the observer. This speed/distance effect correlates with a size/distance effect, namely closer objects appear larger. The two effects together suggest a formal relationship between the spatial and temporal frequency components of a motion-parallax stimulus, such as falling snow. Following the motion plane model of Watson and Ahumada (1985 *Journal of the Optical Society of America A* **2** 322–342) with $w_t = \text{speed} \times w_y$ for a vertically moving stimulus, we observe that speed is inversely related to spatial frequency $(w_x^2 + w_y^2)^{1/2}$ for a motion-parallax stimulus, and that the two equations combine to yield a non-planar surface:

$$w_t = \frac{w_y}{(w_x^2 + w_y^2)^{1/2}}$$

in the 3-D frequency. When such a surface is constructed by using $1/f$ amplitudes and random phases, and the inverse Fourier transform is computed, the resulting image sequence produces a motion-in-depth effect that looks remarkably like falling snow. Besides being an interesting application for computer graphics, this method can also be used to create psychophysical stimuli for studying human motion perception.

◆ **The representation of a moving object in the visual cortex shows peak fMRI activation at its trailing edge**

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The representation of an object in the visual cortex depends predominantly on its retinotopic position. Here, we show that the retinotopic representation of an object in the visual cortex, as revealed by fMRI, was systematically shifted when there were motion signals present in the scene. We presented stationary patches filled with moving texture and measured localised activation in the visual cortex. Perceptually, the patches appeared shifted in the direction of the moving texture. Surprisingly, the representation of the patches in the visual cortex was also shifted by a comparable magnitude—but in a direction opposite that of perception. That is, when a patch filled with moving texture appears shifted in position, there is a region of the visual field (the trailing edge of the moving texture) in which the stimulus is physically present, but does not appear to be present. It is this region that produces peak activation. The pattern of activation could be the result of a deblurring or masking mechanism in which the trailing edge of the stimulus is perceptually suppressed. To test whether there is a mechanism, such as masking, that operates more strongly on the trailing edge of the stimulus, we measured the perceived compression or shift of the trailing edge, compared to the leading edge, of the patches containing motion. There was greater suppression of the trailing edge compared to the leading edge of the patches, suggesting that an asymmetrical process, such as deblurring or masking, is present in the visual cortex.

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◆ **Korte's law, the spatiotemporal sensitivity of vision, and the failure of the proximity principle in apparent motion**

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Apparent motion (AM) is the experience of motion from the successive stimulation of separate spatial locations. According to a classical result of Korte (his third law), spatial and temporal separations (d_s and d_t) between successive stimuli in AM are related directly: if we increase d_s we cannot maintain the same strength of motion without increasing d_t (space–time coupling). Later studies, with better methodology (Burt and Sperling, 1981 *Psychological Review* **88** 171–195) found the opposite: If we increase d_s , we cannot maintain the same strength of motion without decreasing d_t (space–time trade-off). Studies of spatiotemporal sensitivity in continuous motion (Kelly, 1979 *Journal of the Optical Society of America* **69** 1340–1349) suggest that both coupling and trade-off should obtain under different conditions of stimulation. We tested this prediction by measuring the conditions of perceptual equality between different space–time pairs in multi-stable dot patterns called motion lattices. As expected, we found that space–time coupling and trade-off are special cases on a continuum: space–time trade-off holds at low speeds of AM, and space–time coupling holds at high speeds. The proximity principle that holds in the perception of static displays (Kubovy et al, 1998 *Cognitive Psychology* **35** 71–98) does not generalise to AM. In addition, we found that slow speeds are not preferred to high ones (Weiss et al, 2002 *Nature Neuroscience* **5** 598–604).

EYE MOVEMENTS AND PERCEPTION

◆ **When pros become cons for antisaccades versus prosaccades**

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We examined prosaccade versus antisaccade performance for visual stimulation in temporal or nasal hemifields under monocular viewing. Prosaccades were faster after temporal than after nasal stimulation, in accord with previous results. A novel finding was that the opposite applied for antisaccades, consistent with a difficulty in overcoming a stronger prosaccade reflex after temporal-hemifield stimulation. A control study showed that these results were not simply due to antisaccades following nasal stimulation benefitting from being made towards a temporal place-holder. Prosaccades and antisaccades were also compared for visual versus somatosensory stimulation. The substantial latency difference between prosaccades and antisaccades for visual stimuli was nonexistent for somatosensory stimuli, again consistent with antisaccades being slower when a stronger prosaccade reflex must be overcome. Antisaccades can thus benefit when the competing prosaccadic tendency is weakened; but further studies revealed that not all manipulations result in opposite outcomes for the two types of saccade. Although reducing the contrast of visual targets can slow prosaccades and, conversely, speed antisaccades, this was not found at the lowest contrast level we used, where both types of saccade were slowed, thus indicating some common limiting factor on latency. Furthermore, warning sounds presented shortly before a visual target speeded both prosaccades and antisaccades. The results show that several factors which slow prosaccades can speed antisaccades (consistent with competition between different pathways); but also reveal some notable exceptions, where both types of saccade are slowed or speeded together.

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◆ **Compensation for eye movements is partial in perception of both collinear and non-collinear object motion during smooth pursuit**

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During ocular pursuit of a moving target the retinal image velocity of other objects in the visual field differs from their physical velocity. To produce veridical perception of the motion of these objects, the visual system has to compensate for the eye movements. When an object is moving collinearly with the pursuit target, compensation occurs, although incompletely. This partial compensation produces illusions like the Filehne illusion and the Aubert–Fleischl phenomenon (Wertheim, 1994 *Behavioral and Brain Sciences* **17** 293–355). However, whether the visual system compensates for eye movements when an object moves noncollinearly with the pursuit target is

still a matter of debate. We investigated whether compensation occurs in the noncollinear case and whether it is the same as for collinear motion. We measured the perceived motion direction of a moving dot during ocular pursuit (10 deg s^{-1}) of a horizontally moving pursuit target. The angle of the physical motion path of the dot relative to the pursuit path was varied from 0° to 360° . We found that observers made systematic errors in indicating the motion direction. The pattern of these errors was different for a dot moving with a lower (3 deg s^{-1}) than with a higher (8 deg s^{-1}) speed, with larger errors for the lower speed. The data can be explained by a model that assumes that compensation for eye movements is independent of speed and direction of the moving dot. Compensation is assumed to be normally distributed, with mean and standard deviation varying between observers.

◆ **Curved saccade trajectories: Do symmetrical distractors balance the scales?**

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Curved saccade trajectories have been observed in a range of different conditions and can be modulated in direction and magnitude under different experimental conditions. Curvature away from a peripheral location has been observed when subjects orient their attention to a peripheral cue or when a distractor is presented remote from the saccade target. This trajectory modulation has been attributed to inhibitory processes involved in the suppression of a response to the distractor location that results in the saccade being directed initially away from the target location. The spatial extent of this presumed inhibitory process was examined in the present study. In one experiment, the influence of single distractors was compared to that observed when two distractors appeared at mirror-symmetric locations in both visual fields. When a single distractor appeared, saccades curved away from the distractor location; but when two distractors were presented, trajectories tended to be straight. When two distractors were presented at nonsymmetrical locations in both visual fields, trajectories again tended to be straight. In a third experiment, the spatial extent of the inhibitory process was systematically examined by manipulating the target-to-distractor separation. Although there was an effect of side (saccades curved away from distractors) and hemifield (greatest curvature when distractor in target hemifield), there was no clear relationship between curvature and target-to-distractor separation. The findings are discussed in terms of competitive interactions operating in the saccadic system.

◆ **Anisotropy in the eye-movement correlogram**

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The eye-movement correlogram is obtained by reverse correlation of eye velocity with the velocity of a randomly moving target. It resembles an impulse response, typically peaking at a latency between 100 and 200 ms. (The latency increases systematically with decreases in mean luminance and contrast, and is affected by other stimulus parameters as well.) The target moves randomly in two dimensions, and the analysis is performed independently on the horizontal and vertical components. Striking differences are seen in the correlograms obtained in these two directions. Both directions show substantial ringing at 4 Hz, most likely due to an underdamped control system, but the ringing is greater in the horizontal signal, and in the vertical signal the ringing rides atop a positive 'shoulder'. Presumably these differences are due to neurological differences in the innervation of the horizontal and vertical rectus muscles. More detail can be gleaned about these differences from a 'polarisation' analysis. Because it cannot be known for sure that the horizontal and vertical axes of the eye-tracking system are aligned with either the physiological axes, or the axes of the stimulator, individual correlograms are computed for the entire range of measurement angles and stimulator angles (sampled in 10° increments). Next, a principal components analysis is performed on the set of signals. The resulting factor loadings vary sinusoidally with the stimulus angle, but the phase of this variation is different for each component. For the strongest component, the loadings are approximately in cosine phase with the difference between the measurement and stimulator angles, indicating the main effect of alignment between the stimulating and measurement systems.

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◆ **Readers' oculomotor responses to intra-saccadic text shifts**

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Five participants read several chapters of a book while their eye movements were recorded. During occasional saccades, the line of text was shifted to the left or the right by 2 or 4 characters, thus displacing the landing position of the eyes. Although the text shifts were not consciously perceived, they affected the following eye behaviour, particularly changing the frequency of regressive saccades. Leftward text shifts increased regressions; rightward shifts reduced them, relative to a no-shift control condition. Further analyses were conducted to distinguish between alternative accounts for the observed phenomenon. The effect could not be attributed to visual transients from the display change itself, nor to expected changes in the retinal image based on some corollary discharge signal. It did not result from the change in the distribution of landing positions in words. The increase in regressions did not begin until about 175 ms into the fixation. Other possible sources of the effect are discussed, together with their implications for models of eye guidance in reading, and recent research on change detection.

[We would like to thank Gary Wolverton for his great help in setting up the experiment.]

◆ **Event-related prolongation of fixation duration: Evidence for habituation of the intermodal distractor effect**

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When two stimuli are presented at the same time, one being the target and the other an irrelevant distractor, a significant increase of saccadic latency is found. A similar effect can be obtained in free visual exploration of a scene where fixation durations are prolonged by irrelevant visual stimuli. In contrast to the current explanation as an oculomotor reflex (eg Reingold and Stampe, 2002 *Journal of Cognitive Neuroscience* **14** 371–388), we consider the effect rather as a rudimentary manifestation of the orienting reaction, since our data demonstrated that it can also be produced by acoustic distractors (Pannasch et al, 2001 *Vision Research* **41** 3345–3351). However, an orienting reaction should habituate and this has never been shown for the distractor effect. In the actual study, we presented visual and acoustic distractors during free viewing of a sequence of naturalistic pictures. Eye movements and event-related potentials (ERPs) were recorded simultaneously. The data demonstrate a clear distractor effect both in fixation durations and in early components of the ERPs (N1), whereby the effect in ERP components was delayed (by up to 40 ms) relative to the evoked prolongation of fixations. Furthermore, a significant habituation of the visual and acoustic distractor effects has been found not only in the ERPs, but also in visual fixations. These results indicate a good feasibility of the proposed interpretation for mechanisms of the distractor effect.

◆ **Temporal and spatial coupling of selection-for-perception and selection-for-action**

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In vision, selection depends on the salience and attributes of objects in the visual scene. However, selection also depends on the intention to make a movement to a specific region of the space. Here we investigate how selection-for-action and selection-for-perception are related, both temporally and spatially, during the saccade preparation. In our experiments, one of the stimuli was rendered salient by increasing its luminance. Otherwise, the intention to make a saccade towards one of the stimuli rendered it salient. The location of the luminance increment and the saccade target stimulus could either coincide or differ. We used a double-task paradigm in which subjects had to discriminate the orientation of one oblique line presented tachistoscopically within the surrounding distractors at three SOAs from the onset of a preview horizontal display while they were preparing a saccade. Visual selection was measured by the discrimination performance. We found that, more than 100 ms before the saccade, visual selection operates on the basis of stimulus-driven attributes, as the discrimination was influenced only by the luminance of the stimuli. Then, at 50–100 ms delays, the saccade-driven selection process influences visual selection and discrimination performance depends on the actual landing position. The saccade-driven selection operates in parallel with the stimulus-driven selection. However, less than 50 ms before

the saccade triggering, the saccade-driven selection is predominant and the discrimination is at its best at the saccade target position. There, a common saccade target is selected for action and for perception.

◆ **Intrasaccadic occipital gamma burst in humans is preparatory for new fixation**

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Our aim was to quantify gamma-range activity when observers executed voluntary saccades in the dark. We have previously shown V1 activation when observers performed voluntary saccades without visual targets (Bodis-Wollner et al, 1997 *Neurology* **49** 416–420; 1999 *Neurology* **53** 1800–1805). We have also shown that a burst of high-frequency, gamma-range (centred on 37.4 Hz) posterior activity occurs to visual stimuli (Bodis-Wollner et al, 2001 *Clinical Electroencephalography* **32** 139–144) and also when observers execute saccades in the dark to pre-instructed locations. Hence occipital gamma is not necessarily related to current visual input. We recorded EEG in sixteen observers while eye movements and eye position (corneal reflection) were recorded. We applied continuous wavelet transform to the EEG, dividing the perisaccadic period into four segments: preceding, concurrent, and following each saccade, and Hilbert transform to each perisaccadic period of gamma wavelet coefficients. The intrasaccadic EEG was found to contain consistent bursts of gamma starting around 40–50 ms after saccade onset and lasting about 20 ms beyond new fixation. Gamma power is lateralised, depending on saccade direction (left versus right). Gamma has been shown to represent perceptual binding and filling in visual information for a coherent percept. While the exact functional significance of intrasaccadic occipital gamma in the absence of visual targets is not known, it may represent preparatory cortical programming of the coordinates of expected visual input at the locus of new foveation. A sensory ‘preparatory’ function for gamma may be relevant to theories of visual perception of incomplete or missing figures.

◆ **Primary visual cortex activation during intentional saccadic eye movements and shifts in spatial attention**

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Recent evidence indicates that primary visual cortex (V1) is activated during voluntary saccadic eye movements and that on-going stimulus-evoked activity in V1 can be enhanced by attention. Since a saccade is preceded by a shift of spatial attention, we asked whether saccade-related responses in V1 can be distinguished from those caused by voluntary shifts in attention. Using functional MRI together with eye-movement recording, we have examined cortical responses evoked while subjects performed visually guided saccades and compared these responses to (a) those elicited by saccades to instructed locations in the absence of visual targets, or (b) those measured when the subjects shifted their attention while maintaining central fixation. Robust and replicable BOLD responses were found in frontal and parietal eye fields of six subjects in all examined conditions. Primary visual cortex was only consistently activated when saccades were performed, but not during covert shifts of attention, suggesting that V1 is part of the cortical circuit of eye-movement control. The finding that V1 is activated when saccades are performed, irrespective of on-going visual stimulation, suggests that the role of the human primary visual cortex extends beyond that of the classical retinotopic representation of vision.

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OBJECTHOOD 1

◆ **Spatial integration across alternating contrast polarity in even-symmetric and odd-symmetric Gabor lattices**

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In general, dissimilarity of visual elements tends to influence perceptual organisation of an optic scene in terms of segmentation and grouping. Therefore it is surprising that Field et al (2000 *Spatial Vision* **13** 51–66) did not find an effect of Gabor phase jittering in detection of a continuous

path among distractor Gabor patches. Even alternating polarity along the Gabor path yielded only a small effect. We explore here this characteristic of long-range contour integration, and its interaction with continuity and proximity grouping. The experimental paradigm is based on multistable perception of stimuli with a lattice geometry. In this procedure, subjects are asked to report their spontaneous grouping in a lattice of Gabor elements by selecting an icon out of four representing the main lattice vectors. In a previous experiment (Claessens and Wagemans, 2002 *Perception* **31** Supplement, 72), polarity alternations did not degrade grouping strength for lattices of even-symmetric classical Gabor patches, as opposed to control conditions with patches reflecting a radially extending Gabor profile. We conducted an additional experiment in which the lattices consisted of elongated odd-symmetric Gabor elements, thus presenting phase information that is more typical for edge-detector units. The results were entirely parallel to those obtained in the experiment with even-symmetric Gabor elements. Interestingly, grouping odds seem to diverge for different polarity conditions in those lattice geometries for which the absolute distance between aligned elements is small. This hints towards a differential diagnostic value of polarity information in a long-range versus a short-range spatial interaction regime.

◆ **Synergy of elementary visual features in texture segregation**

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A rising amount of studies shows that neural modules for elementary visual features are not independent, but interact in various ways (Wilson and Wilkinson, 1997 *Perception* **26** 939–960). Recent studies claim that there is synergy of different features when they coincide at texture borders (Kubovy and Cohen, 2001 *Trends in Cognitive Sciences* **5** 93–95). Since in previous studies on feature domain interaction objects and borders were confounded, we address the role of both single factors. In our experiments, subjects had to detect texture figures in homogeneous and inhomogeneous Gabor fields. Texture figures were defined by first-order properties (feature contrast in orientation, spatial frequency, or both) with clear texture borders, or were second-order, defined by a difference in the statistical spread of first-order features. For both first-order and second-order figures we find that detection performance is much better than predicted from the assumption of independent feature modules when figures differ from ground in two feature dimensions simultaneously. Further, the synergy effect for first-order texture figures is independent of border length and of the strength of border element feature contrast. Synergy vanishes when figures degenerate to one-dimensional Gabor element arrays or when distributed single Gabor elements were used as targets. Our findings suggest that not first-order feature borders, but object presence is crucial for synergy among feature domains.

◆ **Temporal limitations on extracting global form and binding it with local colour**

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Glass patterns can be created with signal dots of one contrast polarity and noise dots of the opposite polarity. With brief presentations it is easy to identify the pattern but very hard to determine the colour of the signal dots—black or white (Wilson et al, 1997 *Vision Research* **37** 2325–2330). This constitutes a failure to bind global form and local contrast information. In an investigation of the temporal limits of pairing colour with local form, Holcombe and Cavanagh (2001 *Nature Neuroscience* **4** 127–128) found that the colour and orientation of alternating gratings could be correctly paired at rates up to ~18 Hz. However, if the colour and orientation changes were spatially separated, correct pairing was impossible above ~3 Hz. In this study, we first tested the temporal resolution for extracting global form. Alternating Glass patterns could be identified at high rates (~15 Hz), even though the individual patterns were not identifiable in the sum. Apparently, global-form extraction operates with high temporal resolution even though it requires information to be pooled across significant distances. To determine the temporal limits of pairing global form and local colour, we used a stimulus alternating between a Glass pattern of one colour and noise dots of another. The colour of the signal dots could not be identified at alternation rates above 3–4 Hz. Control experiments showed that this temporal cut-off was not due to a limitation on chromatic segregation nor to an inability to identify the pattern itself. Our results suggest that pairing global form with local colour involves a slow, attentional process similar to that for pairing spatially separated local features.

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◆ **Perceptual organisation of Chinese characters: What is the entry-level unit for skilled readers?**

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We have demonstrated in a previous study that learning experience contributes to the perceptual organisation of Chinese characters (Yeh et al, in press *Visual Cognition*). The goal of this study was to further examine the entry-level unit of Chinese characters for skilled readers. We adopted the microgenetic analysis of the primed-matching paradigm (Kimchi, 2000 *Vision Research* **40** 1333–1347) to explore the time course of perceptual organisation of Chinese characters. A prime character was presented first, followed by two target characters after different SOAs, and the participants made speeded same/different judgments to the targets. The prime–target relationship was manipulated so that they either shared configuration similarity or component similarity. Familiarity with the whole character and the sub-character component, as well as the function of the sub-character component (ie a meaning-conveying radical or a sound-conveying phonetic) were also manipulated. Our results indicated an early representation of the component and a weaker and later representation of the global configuration. The semantic radical seemed to be coupled with global structure more than the phonetic component, which may reflect one unique feature of the logographic nature of Chinese characters. These results suggest that the entry-level unit for skilled readers should be the sub-character components, rather than the whole character as has been thought conventionally.

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◆ **Amodal completion—a term stretched too far: The role of amodal continuation**

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The term ‘amodal completion’ has come to be used universally to refer to any situation in which the partial view of an object is treated by the visual system as if the entire object were present for the purposes of perception, identification, search, etc. It is proposed that this term be reserved for situations in which two putative object components are perceptually linked [as in Kellman and Shipley’s figures (1991 *Cognitive Psychology* **23** 141–221)]. It is proposed that another term such as ‘amodal continuation’ be used for cases such as Kanizsa’s half-man figure [Kanizsa, 1979 *Organisation in Vision: Essays on Gestalt Perception* (New York: Praeger)] in which the viewed component is seen as the visible portion of a partially occluded larger object but with insufficient supporting detail for completion. Examples are given from art to support this distinction. It is not merely of terminological interest. The study of the conditions for amodal continuation has been neglected because it is confused with amodal completion. Many cues for occlusion are important in perceiving single elements or sets of non-completable elements as incompletely visible rather than truncated. Data obtained by similar methods to those used by Gillam and Chan (2002 *Psychological Science* **13** 279–283) in their measurements of perceived occlusion are presented, showing some novel determinants of amodal continuation and the way these interact with image components allowing completion. In addition to perceived occlusion at terminating contours, subjective contours are used as a criterion. This is important in eliminating junctions as the critical occlusion cue. Implications of amodal continuation for models of occlusion phenomena, such as physiological models and generic-view approaches are considered.

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◆ **What is a ‘feature’? A meta-analysis of selection criteria for salient visual properties**

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In assessing what counts as a ‘visual feature’, systematic privilege is given to particular classes of stimulus properties over others. Several characterisations of the notion of ‘feature’ have been proposed in specific fields of vision science, yet the use of this notion is not immune from ambiguities. Most studies implicitly assume a number of well-formedness and relevance conditions for selecting features, thus excluding de facto all properties that do not match such criteria. These criteria are not, generally speaking, necessary and sufficient conditions, but rather principles that orient the way in which relevant variables are picked up in experimental settings and modelling. Locality, for instance, plays a major role among these selection criteria, as the current use of ‘feature detectors’ as ‘local neighbourhood operators’ seems to suggest. Other criteria attested in current literature may include: ascribability to objects, compositionality, scalability, invariance across specific conditions, early cortical selectivity, early discriminability, modal specificity, ecological and evolutionary relevance, conscious accessibility. Depending on the particular selection criteria, the notion of feature is then used as a synonym of other, usually much more constrained notions such as ‘channel’, ‘cue’, ‘texton’, ‘visual attribute’. In this paper, I survey the core criteria

employed in vision science for defining what is a 'good' visual feature and I suggest a tentative conceptual classification of what properties of stimuli are considered worth studying. This may contribute to a more constrained research on visual processing and to conceptual clarification of the use of this notion across distinct fields of vision science.

THURSDAY
INVITED SYMPOSIUM 5**PERCEPTUAL LEARNING**◆ **Visual sensory – motor learning in patients and in normal observers**

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Perception is often intrinsically coupled with action, and vision in natural scenes is an active process, given our permanently moving eyes. The relation between perception and action can be modified by training and experience, as in perceptual learning. A well-known example of such changes in sensory–motor coupling is prism adaptation. This modification seems to be based, to a large extent, on modifications of the efferent side, and the cerebellum is thought to play an important role. However, recent studies by, for example, fMRI methods indicate that wearing of prisms not only leads to short-term (motor) adaptations but also to structural changes of afferent cortical signal processing. We investigated the speed and transfer (between the eyes as well as between the arms) of modifications caused by prisms in a pointing task. The prisms shifted the visual world in horizontal direction. We measured the amount of mis-pointing as a function of trial number in a group of more than ten patients suffering from cerebellar disorders, comparing the results with those of a group of healthy observers. Surprisingly, the cerebellar patients ‘learned’ the new task almost as fast as the normal observers, and showed a strong aftereffect after removal of the prisms. These results demonstrate that plasticity of sensory–motor coupling is present even after extensive lesions of the cerebellum. In line with other recent indications of cortical plasticity in adult patients, these results may allow for increased optimism regarding perceptual and sensory–motor rehabilitation of patients after cortical lesions by means of perceptual learning.

◆ **Perceptual learning without perception is not passive**

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The brain demonstrates an amazing ability to become increasingly sensitive to important stimuli. It is often claimed that we become more sensitive only to the critical signals in the tasks we attend to. However, our recent series of experiments had shown that perceptual learning occurs with little attention. First, mere exposure to sub-threshold and task-irrelevant motion coherence signals led to enhancement in sensitivity to the motion direction. This finding indicates that attention is not necessary for perceptual learning (Watanabe et al, 2001 *Nature* **413** 844–848). Second, exposure to two types of task-irrelevant motion that are processed at different levels of visual processing improved sensitivity only at the lower level. These results suggest that task-irrelevant perceptual learning occurs at a very low level (Watanabe et al, 2002 *Nature Neuroscience* **5** 1002–1009). Third, we addressed the question whether such task-irrelevant learning occurs purely passively (caused by stimulus-exposure). During exposure, we presented four different directions of motion an equal number of times, but the direction of interest (DOI) was paired with the task targets. If learning is purely passive, thresholds should improve equally for all the presented directions. Surprisingly, the threshold improved only for the DOI. These results show that learning of a task-irrelevant and sub-threshold feature is not purely passive, but it occurs only when the feature is correlated with a task target (Seitz and Watanabe, 2003 *Nature* **422** 36–37). Based on these findings, a model is proposed in which diffuse reinforcement learning signals perform an important role, complementary to focused attention in perceptual learning.

[I thank Jose Nanez, Yuka Sasaki, and Aaron Seitz for the collaboration in the present study.]

◆ **Treating abnormal visual functions by perceptual learning**

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Practising certain visual tasks leads to a significant improvement in performance, a process termed ‘perceptual learning’. Learning was shown to be specific for basic stimulus features such as local orientation, retinal location, and eye of presentation, suggesting plasticity of the primary visual cortex in adults. However, it is not known whether such a low-level learning has an impact on higher-level visual tasks, like letter recognition. Amblyopia is characterised by several functional abnormalities in spatial vision, including reduction in letter recognition (visual acuity), contrast sensitivity function, vernier acuity, as well as spatial distortion, abnormal spatial

interactions, and impaired contour detection. The visual deficiencies are thought to be irreparable after the first decade of life once the developmental maturation window has been terminated. The vision loss is thought to result from abnormal operation of the neuronal networks within the primary visual cortex, most notably orientation-selective neurons and their interactions. We used perceptual-learning procedure to train this network by efficiently stimulating these neuronal populations and effectively promoting their spatial interactions. This procedure yielded significant improvement in spatial interactions and transfer to higher visual tasks. The training procedure produced a two-fold improvement in contrast-sensitivity and letter-recognition tasks. The results demonstrate that perceptual learning can improve basic representations within the adult visual system that did not develop during the critical period.

◆ **Association field in visual cortical neurons: From subthreshold visual synaptic integration to apparent-motion perception**

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Intracellular synaptic recordings during visual processing show that visual cortical cells have access to a much wider zone of the visual field than that expected from the precision of feed-forward projections. Long-latency subthreshold responses arising from the 'silent' surround result from the integration of visual activation waves spread by slowly conducting horizontal axons within primary visual cortex (Bringuier et al, 1999 *Science* **283** 695–699). The spatiotemporal synaptic integration constraints that can be derived between lateral and feedforward inputs in V1 neurons appear to form strong correlates of perceptual bias measured psychophysically for apparent motion. It has been recently shown that fast apparent-motion sequences of collinear Gabor patches appear for human observers much faster than non-collinear sequences (Georges et al, 2002 *Vision Research* **42** 2757–2772). A study has been carried out of synaptic correlates in intracellularly recorded neurons stimulated along the orientation axis of their receptive field with apparent-motion sequences of co-aligned or parallel Gabor stimuli, sequentially flashed from surround to centre. Simulations based on psychophysical and physiological data suggest that the perceptual bias is most apparent when the feedforward activation produced by the motion signal in the retina travels in phase in the primary visual cortex with the lateral spread of activation (Baudot et al, 2000 *Society for Neuroscience, Abstracts* **26** 446; Séries et al, 2002 *Vision Research* **42** 2781–2797).

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◆ **Asymmetric long-term synaptic plasticity and perceptual learning**

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Recent results on synaptic plasticity indicate that, depending on precise temporal relationship between the activity of the neurons, reciprocal connections between them could be differentially modified in the opposite directions. The functional implications of this type of plasticity are not clear. We describe a mathematical learning rule for a modification of cortical synapses that is inspired by the experimental results and apply it to recurrent networks in the cortex that respond to external stimuli. The model predicts that repeated presentation of the same stimulus leads to saturation of synaptic modification, such that the strengths of recurrent connections depend on the configuration of the stimulus but not on its amplitude. When a new stimulus is introduced, the modification is rekindled until a new equilibrium is reached. This effect may explain the saturation of perceptual learning when practicing a certain task repeatedly. We present simulations of contrast discrimination in a simplified model of a cortical column in the primary visual cortex and show that performance of the model is reminiscent of recently discovered context-dependent perceptual learning.

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◆ **The neural basis of perceptual learning**

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The specificity of perceptual learning suggests the involvement of early stages in cortical processing. The underlying mechanism must accommodate not only a specificity for location and orientation, suggesting the involvement of early, retinotopically mapped visual cortical areas, but also for context or stimulus configuration, requiring specificity for complex stimulus shapes. The requirement for encoding information about stimulus shape in early cortical areas depends on the nature of the stimuli that are discriminated and on the behavioural context of the discrimination. Shapes of intermediate complexity that have to be identified rapidly and in parallel with other shapes may require representation at early stages in visual cortical processing. Imaging studies

in human subjects demonstrate the reorganisation of activity across the visual pathway with shape training, with an increased level of activity in early retinotopic cortex including V1 and V2, a decrease activation of lateral occipital cortex, and a decrease in the dorsal attentional network including posterior parietal and premotor regions. Studies in non-human primates trained on a shape-discrimination task show, at the level of single cortical neurons in V1, specificity for the attributes of the trained shape that reflects the contextual specificity of the learning. These properties are subject to top-down influences, since they are seen only when the animal is performing the trained task. The contextual influences for the same cell change radically from trial to trial as the animal performs different perceptual tasks. The properties of V1 are therefore likely to reflect an interaction between local circuits and top-down influences mediated by feedback from higher-order cortical areas.

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INVITED SYMPOSIUM 6

THE EXPERIENCE OF SEEING: PHYSIOLOGY, PSYCHOPHYSICS, AND PHILOSOPHY

◆ The need for communicability of conscious experience

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Everyone at this meeting appreciates that our knowledge of the outside world results from complex computations based partly on sensory messages and partly on assumptions and experiences not contained in those messages; the physical stimuli from the real world provide the sensory input only for the computation, not for the whole of our perceptual experience. I suggest that: (i) There is an additional demanding requirement that has to be met before we consciously experience the results of the computations, namely the representation of these results in a form that can be readily communicated to other people. (ii) Conscious experience has to be communicable for it to make its main contribution to survival of the species: explaining our experiences, decisions, and actions to other people is essential for our form of social life, and the form of our social life must have been an important factor in the global expansion and evolutionary success of our species over the last hundred thousand years or so. (iii) If the survival value of conscious experience results from its communicability, this would have influenced the nature of conscious experience itself, so that we would tend to be aware only of what is readily and unambiguously communicable to others. Several well-known features of the experience of seeing may fit in with this view.

◆ Psychophysics combined with fMRI/TMS to reveal cross-modal integration and hidden visual computation

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Techniques such as fMRI and TMS define a new era of psychophysics. Whereas simply adding these techniques to classical paradigms is relatively straightforward, it is still a struggle to find what issues may be effectively addressed and by which combinations of techniques. We have found it particularly fruitful to exploit discrepancies between sensory input and the conscious percept. In the illusory-flash illusion (Shams et al, 2000 *Nature* **408** 788), a single flash with two sounds is perceived as multiple flashes. We compared EEG/fMRI signals in trials where illusion occurred versus when it did not. Though the stimuli were physically identical, modulation of neural activity by sounds was found in V1, V2, and V3 only in the illusory-flash trials. Moreover, the loci and dynamics of visual cortical activity in the illusory-flash trials were very similar to those recorded during a physical double-flash condition (Shams, et al, 2001 *NeuroReport* **12** 3849–3852). In another fMRI study we employed the slit-view paradigm, where an object translates behind an occluder. Though the object is visible only through a narrow slit aperture, it is often perceived as a whole. At what level in the visual pathways does neural activity correspond to the conscious percept of wholeness? We found that MT and IT activity correlated with the whole percept, whereas V1 activity did not (Yin et al, 2002 *Current Biology* **12** 1–20). Unlike fMRI, TMS is a more active technique with a higher temporal (and a lower spatial) resolution. We used it to reveal artificial scotoma and backward filling-in (Kamitani and Shimojo, 1999 *Nature Neuroscience* **2** 767–771) as well as hidden, and accurate cortical representations of location in the flash-lag paradigm (Wu and Shimojo, 2002, VSS abstract 15). To sum, the devising of effective psychophysical paradigms remains essential to taking full advantage of advanced technology.

◆ **Seeing and perceiving: Phenomenology and physiological mechanisms**

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Although the brain mechanisms underlying perceptual organisation have long been a central quest in vision research, they still remain poorly understood and continue to be a topic of intensive research and debate. Over the past ten years records have been made of the activity of cells in the visual cortex of monkeys trained to report what they perceive when viewing perceptually rivalrous stimuli, which are known to instigate a continuous reorganisation of perception. In any studied area, only a fraction of neurons was found to respond in a manner that reliably reflects shifts in perception. This small number of neurons is distributed over the entire visual pathway, rather than being part of a single area in the brain. Of the areas studied, the inferior temporal (IT) cortex of the temporal lobe was found to have the highest number of perception-related cells. Notably, a tight relationship between IT activity and the animal's perception was clearly evident also in experiments in which monkeys were trained to look for and identify familiar targets embedded in natural scenes. During exploration, neuronal activation began shortly before effective targets were fixated, but only if the target was the goal of the next fixation. I briefly summarise these results and continue with the description of rivalry experiments in which both local field potentials and multiple unit activity were measured with multiple electrodes, placed over more than one visual area. Of interest is the study of covariation of activity within and between various occipito-parietal areas under different stimulus and perceptual conditions. Analysis of data collected in such experiments, revealed significant coupling between distant sites both in non-stimulated and in stimulated conditions. While these patterns were consistent and robust, stimulus-specific differences were subtle. During rivalry, covariation patterns were significantly diminished, and in some cases completely disappeared. These findings suggest that the coherence in the response of visual neurons during rivalry may be related to system's stability rather than to the perceptual state of the animal. Finally, psychophysical experiments are described which examine the relation of the process of stabilisation of ambiguous percepts with perceptual memory.

◆ **Rapid visual processing and the experience of seeing**

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There is increasing evidence that high-level visual representations can be activated by highly automatic mechanisms that operate very rapidly and in the near absence of attention. Neurons in the temporal lobe highly selective to complex visual forms can respond at such short latencies that anything other than a feedforward pass is almost excluded in the time available. And the existence of ultra-rapid visual categorisation in both humans and monkeys suggests that the initial responses of such neurons can be used almost directly to drive behavioural responses with very short reaction times. Simulation studies with SpikeNet (an image processing system that uses very large arrays of asynchronously spiking neurons) demonstrate that it is perfectly possible to produce selective responses to almost any visual form with simple feedforward mechanisms that can operate when only a tiny fraction of the available neurons has had a chance to fire. However, the fact that a feedforward pass through the visual system can result in highly selective visual responses and rapid behavioural reactions does not mean that this is all there is to vision. Many aspects of visual perception will depend on feedback from higher levels. For example, bottom–up image processing techniques are notoriously inadequate for tasks such as scene segmentation and figure–ground segregation, but rapid activation of high-level representations could be used to drive intelligent segmentation via top–down projections. Thus the complete visual experience that we have when we perceive a scene will depend on complex interactions between bottom–up and top–down mechanisms. Nevertheless, it seems clear that pure feedforward mechanisms are capable of doing considerably more than has been suspected in the past.

◆ **Cortical sites and mechanisms of two types of visual experience**

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Everyone is aware of a strange dichotomy of visual experience: rapid 'vision at a glance' and a slower 'vision with scrutiny'. On the one hand, we are able to perceive complex images, objects, categories and scenes even when these are presented briefly or at very rapid rates (RSVP). On the other hand, we are surprisingly unable to report details outside the focus of our attention, large changes in flashed pictures (change blindness), and even the viewpoint of recalled objects. We suggest that bottom–up processing is implicit, and that perceptual consciousness only begins

when visual information reaches post-processing high cortical levels. Thus, rapid conscious vision with spread attention is attributed to the large receptive fields of high-level cortical areas, where neurons respond to complex images but generalise over—ie are insensitive to—precise object location, orientation, size, lighting, or the particular details that originally formed the represented category. In contrast, slower perception with focused attention is seen as a conscious return to lower cortical levels following reverse-hierarchy feedback connections to the sources of higher-level activation, recovering detailed information available in the specialised receptive fields found there. The dual correspondence is especially apparent in two types of visual search: spread-attention feature-search (perceiving ‘what’ without ‘where’), deriving from high-level position-insensitive receptive fields, versus scanning-attention or conjunction search deriving from the return to low-level position-encoding receptive fields. Physiological data support this reverse hierarchy theory and the characteristics of the two perceptual modes indeed match those of higher and lower areas, respectively.

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◆ **On comprehending the sensory effects of movement: Toward a theory of perception and consciousness**

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We offer a theoretical framework for understanding intermodal and intramodal differences in the qualitative character of perceptual states. We ask whether the same thinking can be extended to account for the question why some states have any perceptual qualitative character at all. In this way, our account seeks to bridge the explanatory gap for perceptual consciousness. The discussion builds on works by O’Regan and Noe (2001 “A sensorimotor account of perception and perceptual consciousness” *Behavioral and Brain Sciences* **24** 883–975), and by Noe [forthcoming, *Action in Perception* (Cambridge, MA: MIT Press)]; and also by O’Regan and Noe [forthcoming, *Perception and Consciousness: A Sensorimotor Approach* (Oxford: Oxford University Press)]

ORAL PRESENTATIONS

MOTION—HIGH LEVEL

◆ **On the principle of minimal speed difference for the stereokinetic effect**

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In the stereokinetic effect, a 3-D structure is perceived when a 2-D figure is rotated in the image plane. To account for this, Zanforlin and colleagues have proposed a mathematical model that minimises relative speed differences between stimulus points. They achieve this by adding a velocity depth component to each stimulus point so that the speed difference between any two stimulus points is minimal. They claim that the 3-D structure derived from this 3-D velocity field predicts the stereokinetic percept. I question the mathematics of this model, and prove that its mathematics is incorrect in all cases of applications of the model in the literature, each to a specific stereokinetic phenomenon. A simple, yet representative, example is a bar rotating around its centre in the image plane (Beghi et al, 1991 *Biological Cybernetics* **65** 425–432). Beghi et al reported that the percept is a rotating bar with a constant tilt in depth. They applied the model by adding a velocity component in depth to each point of the bar so that all points have the same speed. However, since the centre of the bar necessarily has zero rotational speed, it has to be credited with the biggest velocity component in depth. This means that the bar, at the middle, has to be either bent when all points have the same velocity direction in depth, or broken when the two halves of the bar move in opposite directions in depth. Either way, this is incompatible with the reported percept. This problem can be avoided partially if a new coordinate system is chosen that sits at one end of the bar. However, in the world coordinate system, the equal speeds established in the new coordinate system are no longer equal; and there is no justification for this new coordinate system to be perceptually privileged. Regardless of the coordinate system, the bar will keep deforming itself since, at any location along the bar, the added speed in depth is constant over time.

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◆ **On the distortion of perceived motion: Explaining the Pavard and Berthoz effect and the Freezing illusion**

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Pavard and Berthoz (1977 *Perception* **6** 529–540) reported that when an observer is abruptly moved passively on a cart while watching a pattern scrolling at a constant velocity across the eyes in a head-mounted display, the pattern appears to suddenly stop moving. The illusion is asymmetric: it is very strong when the pattern moves across the display in the direction opposite to that of the passive body-motion, but ambiguous when it moves in the same direction. More recently Mesland and Wertheim (1996 *Vision Research* **36** 3325–3328) reported a somewhat similar phenomenon: when we look at a pattern scrolling at a constant velocity across a monitor screen, and the monitor itself is moved in space, the pattern appears to freeze on the screen. This Freezing illusion (shown during the presentation) is also asymmetric: it is strong when monitor and scrolling pattern move in opposite directions and ambiguous when they move in the same direction. At the time of their publication, these illusions could not be easily explained, but now a quite simple explanation can be presented. It is based on the assumption that the perceived velocity of a stimulus always corresponds to the difference between two neural signals minus the just noticeable difference (JND) between them. In the case of the Freezing illusion these two signals are the retinal velocity signal of the scrolling pattern across the monitor, and the retinal velocity signal of the moving monitor. With the Pavard and Berthoz effect, they are the retinal velocity signal of the pattern and the vestibular self-motion signal. It is shown how the sign of the JND causes the asymmetry as well as the reported ambiguities in both illusions, why they are independent of eye movements, and why they appear as a confusion of egocentric and exocentric frames of reference.

◆ **Biological-motion discrimination by form analysis**

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It is commonly believed that brain areas specialised for the perception of biological motion exist, even though the underlying brain mechanisms are still little understood. Biological-motion perception is usually regarded as a specialised form-from-motion estimation. Results of a recent study by Beintema and Lappe (2002 *Proceedings of the National Academy of Sciences of the USA* **99** 5661–5663) suggested that local image motion is not required for the perception. We developed an ideal-observer model which focused exclusively on the form information available in a biological-motion stimulus. The model uses a library of snapshots of a walking human person which are stored internally and serve as the model's conception of a walker. By matching frames of the stimulus to these templates, the model is able to choose the pose of the walker and draw a decision in a given task. Thereby, only form information is used, with all motion signals ignored. We tested the model by comparing its performance in different 2AFC tasks with psychophysical data. For the stimulus, we used a limited-lifetime point-light walker whose dots were repositioned randomly on the body's limbs depending on their lifetime. This way we developed various 2AFC-discrimination tasks in which we varied the contribution of form and motion information independently. In all tasks, model and human observers showed striking similarities in their dependence on the number of points and point lifetime. Since the model is relying on form information only, the results indicate that these often-used discrimination tasks can be solved without local motion signals when a threshold of total number of points per trial is exceeded, strengthening the new conception that the perception of biological motion may rely on a sequential form analysis rather than on local motion signals.

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◆ **Representing biological motion**

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Recently, we have been using a novel spatiotemporal morphing algorithm (Giese and Poggio, 2000 *International Journal of Computer Vision* **38** 59–73) to explore the mental representation of biological-motion patterns. We presented observers with animated patterns of point lights corresponding to trajectories generated by spatiotemporal morphing between three prototypical human locomotion patterns: walking, running, and marching. The seven patterns obtained from this morphing procedure were organised into stimulus spaces corresponding either to a (T)riangle or

an L-shape. For each configuration, observers were asked to judge the similarity between all pairs of stimuli using a comparison-of-pairs paradigm. A measure of perceived dissimilarity computed from these judgments was submitted to multi-dimensional scaling. The perceived structures recovered in this way closely matched the original stimulus structures. This suggests that the visual system represents related categories of locomotion in a common metric space, reflecting the spatiotemporal similarity of motion trajectories. Here, we relate these findings to previous research using static shape categories (eg Cutzu and Edelman, 1998 *Vision Research* **38** 2229–2257) and in particular to the results of a recent simulation study. In this latter study, we used the neural responses of a physiologically plausible model of biological-motion recognition (Giese and Poggio, 2003 *Nature Reviews Neuroscience* **4** 179–192) to recover metric structures which also closely resembled the original stimulus structure. Implications of these simulation results for our understanding of biological motion processing are discussed.

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◆ **Attending to weak visual motion activates separate brain regions from attentional tracking**

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Seeing a low-contrast object in motion in the visual periphery depends upon attentive resources to boost the weak visual signal. Focused attention is also used to follow an object as it moves in the periphery, called attentional tracking, which involves moving attention through space as an object moves. fMRI was used to measure brain activity during these two visual tasks to determine their neural separability. Attending to motion and attentional tracking can be separately invoked when viewing two superimposed radial gratings, one luminance and one colour grating, rotating around a fixation point in opposite directions (Cavanagh, 1992 *Science* **257** 1563–1565). Here, luminance gratings were presented at low contrasts (1.5% to 3.5%), so that the motion was difficult to see and demanded constant attention. Presented at 60% contrast, the red and green components of the colour grating were easy to see, but the motion was only visible when observers attentively tracked a particular component. In each trial, observers discriminated a speed change of one of the gratings (standard speed 1.5 Hz, change ± 0.4 Hz). Results showed that different areas exhibited increased activity while observers attended to weak luminance-grating motion than in attentive tracking of the colour grating. Frontal areas, including inferior frontal sulcus, anterior insula, and paracingulate cortex, were more active during the more demanding task. Bilateral superior parietal and superior frontal areas (including frontal eye fields) were more active during attentional tracking. These results suggest that attention mechanisms for boosting visual signals may depend on different brain regions than attentively tracking an object through space.

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◆ **fMRI reveals the neuronal substrate underlying form and motion processing in transformational apparent motion**

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Transformational apparent motion (TAM) occurs when a figure changes discretely from one configuration to another overlapping configuration. Rather than an abrupt shape change, the initial shape is perceived to transform smoothly into the final shape as if animated by a series of intermediate shapes. Here fMRI has been used to determine the neurophysiological substrate of this motion illusion. In the past, fMRI has been used both to locate areas of the human brain involved in processing form and to locate areas involved in processing motion. Relatively few researchers, however, have examined how the form and motion processing streams interact. For this purpose, TAM [Tse and Cavanagh, 1995 *ARVO*; Cavanagh and Nakayama, 1998, in *High-level Motion Processing—Computational, Neurobiological and Psychophysical Perspectives* Ed. T Watanabe (Cambridge, MA: MIT Press) pp 249–266] is an ideal stimulus probe, because the direction of motion that is perceived depends on the form relationships that exist between successive stimuli (Tse and Logothetis, 2002 *Perception & Psychophysics* **64** 244–265). In two experiments, TAM stimuli and control stimuli that were similar in low-level properties, but which did not give rise to the perception of TAM, were blocked. The BOLD signal was measured with a 1.5T GE scanner. Voxel volume was $3.75 \times 3.75 \times 5 \text{ mm}^3$ in 25 horizontal slices collected with single-shot T2* weighted gradient-recalled EPI sequences. When TAM and non-TAM stimuli were contrasted with the general linear model, there was significantly more BOLD signal in the following areas bilaterally: areas 18 and 19, area MT+, and area 7 in the superior parietal lobule and precuneus. These data are consistent with models that place a stage of texture and form analysis in extrastriate cortex before motion processing in area MT+.

CLINICAL

◆ Dorsal pathway activation during visuo-spatial imagery in early blind subjects

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Positron emission tomography (PET) was used to compare the functional anatomy of visuo-spatial imagery between early blind and sighted subjects. Subjects were instructed to generate a mental representation of verbally provided patterns that were placed in a grid, and to assess subsequently the pattern symmetry in relation to a given grid axis. Results showed that the visuo-spatial imagery task, when contrasted with a verbal memory control task, activated similar areas in early blind subjects and in blindfolded controls. The precuneus (BA 7), superior parietal lobule (BA 7), and occipital gyrus (BA 19) were involved. Behaviourally, results obtained for this task showed no significant differences between blind and sighted subjects in terms of performance. Both groups performed at the same level, but with two different strategies. The blindfolded sighted subjects used a visual strategy, while blind subjects coded each square of the grid in an $X-Y$ coordinate system. Results support the hypothesis that visuo-spatial mental imagery activates 'visual' associative areas in early blind subjects as well as in sighted subjects. The dorsal pathway seems to be involved in visuo-spatial imagery in early blind subjects indicating that this pathway undergoes development in the absence of vision.

◆ Detection of visual processing in cortical blindness: The importance of specific stimulus parameters

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In some cases of cortical blindness, the ability to detect certain visual stimuli presented within the field defect remains. We have previously reported the presence of blindsight in eight out of ten cortically blind patients studied. Using a temporal 2AFC paradigm we have systematically investigated the detection of spatially and temporally modulated Gabor patches presented within the blind field of ten cortically blind patients. The spatial and temporal frequency ranges investigated were 0.5 to 7.0 cycles deg^{-1} , and static to 33 Hz, respectively. The Gabor patches were limited in spatial extent to 4 times the standard deviation of the spatial Gaussian (SDsg). The effect of stimulus size was also determined by measuring discrimination score as a function of stimulus size (SDsg of Gabor range between 0.5 and 3 deg). The spatial channels mediating blindsight in all 8 cases were optimally sensitive to low spatial frequencies (0.5–2 cycles deg^{-1}) with no significant responses above 4.7 cycles deg^{-1} . The temporal channel in 4 out of 5 cases tested showed optimal responses between 5 and 20 Hz. The stimulus size resulting in above threshold (75%) detection was variable between 6 cases studied (SDsg ranged between 0.8 and 2.6 deg). The two negative cases of blindsight performed at chance level under all stimulus conditions tested. The narrow width of the spatial and temporal channels demonstrates the importance of specific stimulus parameters and shows how cases of blindsight could be overlooked. The data are also discussed in relation to lesion characteristics, age of onset, and aetiology. [Chief Scientist's Office, Scottish Executive (CZB/4/30).]

◆ Colour correspondence in cortical colour blindness

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Cerebral achromatopsia, or cortical colour blindness, is a rare condition that results from damage to the ventromedial area of the occipital cortex. Despite the loss of colour experience, such patients can still use wavelength variation to perceive form and motion. We report two experiments in which we examined whether colour can also orient exogenous attention in an achromatopsic observer. We employed the colour-correspondence paradigm in which attention is drawn from one coloured stimulus to the location of a subsequently presented stimulus that shares the same chromatic identity as the first. In normal observers, this induces the perception of motion between the two chromatically matching stimuli. In experiment 1, an achromatopsic observer performed a reaction-time task in which he responded to the onset of a target letter that could appear either at a location corresponding with the apparent motion or at a non-corresponding location. Results showed that targets were detected more rapidly when presented at a colour-correspondent location. This suggests that, although the patient does not consciously perceive the apparent

motion observed by normal participants, the same orienting of attention between corresponding colours occurred. Experiment 2 revealed that the effect is abolished when the chromatic borders of the inducing stimuli are masked with luminance contrast. We argue that the effect is dependent on chromatic contrast mediated via an intact parvocellular pathway.

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◆ **Impairments of goal-driven and stimulus-driven control in patients with right fronto-parietal lesions**

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We explored oculomotor capture in patients with right-hemisphere cortical and subcortical lesions. Subjects searched for a coloured target among three distractors and signalled its location with a saccade. An additional irrelevant distractor was presented either on the left or the right. This distractor appeared either with or without an abrupt onset and was either similar to or dissimilar from the target (see Ludwig and Gilchrist, 2002 *Journal of Experimental Psychology: Human Perception and Performance* **28** 902–912). In comparison to twelve age-matched healthy control subjects, saccades of three patients with right cortical lesions showed significant increases in overall capture as well as increased onset-based capture. One of the cortical patients, with an isolated frontal lesion, also showed an overall increase in similarity-based capture. None of the three subcortical patients was significantly different from controls. For the cortical patients these effects were also spatially modulated. The level of capture was reduced when the target was on the right and the irrelevant distractor was on the left. In this study, we were able to assess both stimulus-driven and goal-driven contributions to visual selection in a single paradigm. All three cortical patients showed a general reduction in selection control and increased sensitivity to stimulus-driven factors. In addition, the right frontal patient showed an increased sensitivity to goal-driven factors.

◆ **Computational models and occupational vision standards for acuity and contrast sensitivity**

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Using aircraft maintenance as an example, we describe a way of using image discrimination models to assist in the development of performance-related occupational vision standards. First, we calibrate a simple image discrimination model so that it accurately predicts a subset of the ModelFest stimuli that are most similar to the original and blurred images of interest, airframe, and powerplant cracks. We then predict the visibility of cracks varying in length and width viewed by observers having various simulated visual acuities and contrast sensitivities. Poor visual acuity is simulated by increased Gaussian blur of the images. Poor contrast sensitivity is simulated by broadband reduction in contrast. The simulation results allow performance requirements described in terms of physical images to be translated into acuity and contrast sensitivity standards. Variables such as age may be brought into this framework through previous studies relating those variables to the contrast sensitivity function.

◆ **Validation of a simulation of visual impairments**

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We aimed to develop and validate an image transformation that gives normal observers a good impression of the visual perception of an impaired subject. We used the simulation method described by Peli (eg 1996 *Journal of the Optical Society of America* **13** 1131–1138) in which the image is split up in a range of (one octave wide) frequency bands (by using a Laplacian pyramid). A local contrast image is derived for each frequency band, and features with contrasts below a certain threshold are removed from the image. We first measured contrast thresholds for detection and orientation discrimination of Gabor patches. We then measured below which local contrast level features could be removed from a natural image (a face). Subjects discriminated the transformed image from the original in a 2AFC experiment. We used simulations in which single frequency bands were transformed, as well as multiple band transformations to establish the relationship between contrast thresholds for Gabors and the local contrast threshold values that

should be used in a simulation of natural images. The centre frequency of the (high) frequency band that could be fully removed from the image was found to be higher than the acuity limit from detection of Gabors (probably owing to the large bandwidths). The contrast threshold of low-frequency bands used in the simulation was higher than the detection and discrimination thresholds for Gabors (possibly owing to masking effects). We conclude that the thresholds that should be used in the simulation are not simply the same as detection or orientation discrimination thresholds of Gabors. The newly found relationship between sensitivity to Gabors and the local contrast in natural images can be used to give insight into the information visually impaired people are lacking.

COLOUR†

◆ On the reproducibility of rod single-photon responses: The Gordian knot of phototransduction unravelled

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At absolute scotopic threshold, individual rods are absorbing photons at intervals of at least several minutes [Rodieck, 1998 *The First Steps in Seeing* (Sunderland, MA: Sinauer Associates) pp 136–137]. Such performance requires single-photon responses (SPRs) reliable enough, and with adequate signal-to-noise ratio for useful visual performance. For the last 25 years, it has been an abiding problem in photoreceptor physiology to reconcile the reproducibility of SPRs with the inherently variable nature of all molecular reactions. In particular, SPRs in vertebrate rods are much less variable than expected if isomerised rhodopsin (R^*) inactivated in a single step, and no other variability-reducing mechanisms were available. Several models have been proposed to account for SPR reproducibility, none of which can, alone, account for a broad range of rod dim–flash responses while being based on known biochemistry. We present a new stochastic model of phototransduction ('sequential phosphorylation, or SP model'), the core of which is sequential ratcheting down of R^* activity by multiple phosphorylation (P_n) of R^* , and a concomitant P_n -dependent increase in the probability of final R^* shut-off by arrestin (Arr). We evaluated the model by Monte-Carlo simulations of dim–flash responses, and compared its behaviour with that of a large set of original dim–flash response data (Whitlock and Lamb, 1999 *Neuron* 23 337–351). With 8 steps of R^* inactivation (7 P_n steps + Arr), the SP model accounts for observed SPR reproducibility (a prior model hypothesised the need for 10–20 steps), and can reproduce key electrophysiological data, including salient features of responses from rods in which R^* inactivation was disrupted by genetic manipulation. The evolutionary significance of SPR reproducibility and the 'design' of the mechanisms that support it are discussed.

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◆ Colour appearance in mesopic conditions

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Twelve observers used the magnitude-estimation technique to make judgments of the lightness, colourfulness, and hue of circular test colour patches presented in Mondrian displays on a CRT monitor. Forty different test colours were presented at the centre of the screen with two adjacent reference patches for white and colourfulness and a grey background of 20% luminance. Ten colours were repeated in each session to check the intra-observer consistency, making a total of fifty test colours. Each display was presented as a static image with a viewing distance of approximately 60 cm. The observer's visual task was not constrained, ie not fixated on the test patch. The experiment was repeated ten times, for two field sizes (2 deg and 10 deg) and five luminance levels (white of 87.4, 8.9, 1.0, 0.097, and 0.0094 cd m^{-2}). Observers were kept in the experimental room for 25 min to adapt fully before commencing observations. The reduction in luminance level was achieved by fitting one, two, or three large sheets of neutral density filter, of density 0.9, over the monitor faceplate. All test colours were measured with a Photo Research PR-650 spectroradiometer directly from the screen. Analysis of the results across the eight phases shows a significant effect of rod contribution to the visual attribute of (achromatic) lightness, especially for the 10 deg test-field size, and lesser effects on colourfulness and hue. The accuracy of the Hunt'94 colour appearance model in predicting the results was investigated. Also the

† In memory of Dick Cavanious.

discrepancies of predictions of purely photopic models of colour appearance, such as CIE CAM97s, were considered. It is concluded that, for typical viewing conditions in cinemas and conference presentations, rod contributions to perceived lightness cannot be ignored.

◆ **Comparison of spatial integration of S-cone-selective luminance increments and decrements with retinal structure**

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It has been shown previously (Vassilev et al, 2001 *Perception* 30 Supplement, 17–18) that the sensitivities to S-cone-selective luminance increments and decrements depend differently on the retinal eccentricity and stimulus size, a finding supporting the existence of separate S-cone ON and OFF pathways. In the present work, Ricco's area of complete spatial summation was measured as a function of stimulus polarity and retinal location. The data were compared with known human retinal morphology. The two-colour threshold method of Stiles was applied to selectively stimulate the S-cones. A small amount of blue light (12–40 td) from a monitor was added to the intense yellow background (4000–30 000 td). The test stimulus was blue luminance increment or decrement within a circular area of variable size. It was presented at 0° to 20° along the temporal retinal meridian. Ricco's area was nearly constant and approximately the same within the 0°–5° range and increased beyond this range, the decremental area becoming larger than the incremental in the periphery. The comparison with morphological data in the 5°–20° eccentricity range have shown that: (a) the number of S-cones within a Ricco's area increases with eccentricity from about 10 to 40 for increments and 10 to 90 for decrements; (b) Ricco's area for increments and decrements increases faster than the dendritic field of the S-cone ON cells (small bistratified cells, SBC); (c) approximately 2 to 4 SBCs are included within an incremental Ricco's area. We assume that, if S-cone luminance decrements are detected via separate OFF cells, these should differ in density and dendritic field size from the S-cone ON cells at the retinal periphery only.

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◆ **Colour detection, discrimination, and hue in the (S, M) and (S, L) planes of colour space**

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Anatomical studies have revealed two qualitatively distinct pathways that carry S-ON and S-OFF signals. Recent psychophysical findings on S-cone increment (S+) and decrement (S–) detection suggest functional distinctions between these two pathways. We performed detection, discrimination, and colour scaling procedures in the (S, L) and (S, M) planes of cone contrast space in order to study the long-wave cone inputs to S+ and S– mechanisms. Approximately equiluminant, $L = -M$, noise was used to reduce the sensitivity of the red and green mechanisms. The detection data were used to estimate cone weights into detection mechanisms, and the discrimination data were used to test the detection model. Here we emphasise the hue-scaling results. The '4 + 1' method (Gordon et al, 1994 *Perception & Psychophysics* 56 27–41) was used to scale the percentage of red, green, yellow, blue (summing to 100%), and saturation of the stimuli. As expected, saturation was approximately constant for all these threshold-level stimuli. Each of the other colour scales roughly followed the predicted pattern for linear mechanisms. The relationship between detection and hue is not straightforward for mechanisms detecting S+ or S–; in particular, the scaled values for 'yellow' are lower than 'blue' ones, although both sets of stimuli were at threshold.

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◆ **Spectral bandwidths of colour detection mechanisms revisited**

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Recent psychophysical studies disagree whether higher order (possibly, nonlinear) mechanisms participate in chromatic discrimination. D'Zmura and Knoblauch (1998 *Vision Research* 38 3117–3128), using a chromatic analogue of critical-band masking in the equiluminant plane, reported evidence for linear mechanisms intermediate to cardinal L–M and S axes. Nevertheless, their results were criticised (Sankeralli and Mullen, 2001 *Vision Research* 41 53–55) on the basis that the chromatic signal axes investigated were too close to the cardinal axes to differentiate cardinal from intermediate mechanism contributions. We repeated their experiment including a test along an intermediate axis expected to be the most sensitive to departures from linearity. Threshold-versus-noise curves were measured along L–M, S, and an intermediate axis, estimated as midway between the former two in threshold units, in the presence of sectorised noise centred

on the signal direction. The signal was a Gaussian temporal pulse ($\sigma = 160$ ms) modulated over a Gaussian region of the screen ($\sigma = 2.5$ deg), presented in a 2AFC paradigm and varied over trials via a double-random staircase. Three sector half-widths were tested (0° , 30° , 60°). For each axis, the hypothesis that detection was mediated by a linear mechanism tuned to this axis was evaluated by comparing the fits to the data across different noise-sector widths with individual or a common threshold-versus-noise curve. The analyses exclude detection models based on linear off-axis and narrow-band axial mechanisms and support the participation of linear mechanisms intermediate to the cardinal axes.

◆ **Classification images for chromatic signal detection**

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The number and nature of the mechanisms for the detection of coloured stimuli is still unclear. Our goal here was to test whether there exist higher-order colour mechanisms, tuned to specific directions in colour space that lie intermediate to the three-colour opponent 'cardinal' directions in colour space. In a yes/no experiment, subjects had to detect the presence of a low-contrast signal in visual chromatic noise. The noise pattern consisted of 24×24 square patches of light. Each noise square subtended 0.5 deg of arc and was assigned a colour drawn randomly from the isoluminant plane of DKL colour space. The signal consisted of a centrally presented square of uniform colour subtending 8×8 background patches. The signal colour was chosen either along the red–green or yellow–blue cardinal axes or along the main diagonal of the isoluminant plane. From the observers' "yes" and "no" responses, classification images were computed for each signal colour. Colours of resulting classification images were projected onto radial axes of different azimuths in DKL colour space to assess the contributions of the different colour directions to detection. In all cases, the variances of the projected classification images were highest within $\pm 10^\circ$ of the respective signal colours. This implies the contribution of higher-order (intermediate) mechanisms to signal detection.

LIGHTNESS, BRIGHTNESS, SHADING, TRANSPARENCY 1

◆ **Lightness specific processing occurs at low spatial frequencies**

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The relationship between edge detection, identification of polarity, and the perceived lightness pattern was examined. The stimulus was a step edge masked with a high-contrast sinusoidal grating (spatial frequency 0.45 – 12 cycles deg^{-1}), occurring either in-phase or 180° out-of-phase with respect to the edge. In the first experiment, detection and identification thresholds were measured with a 2AFC paradigm. The masking tuning functions, peaking around 2 cycles deg^{-1} showed only minor differences between (i) detection and identification performance and (ii) the two masking conditions. In the second experiment, the subject adjusted the contrast of the step such that the lightness difference between the two sides of the edge was just visible. In the in-phase condition, the masking tuning function for the lightness pattern was roughly a vertically shifted version of the detection curve, suggesting that lightness pattern was visible at detection threshold but the criterion was higher in the subjective task. However, in the out-of-phase condition low-pass behaviour was observed. Below 2 cycles deg^{-1} , contrast thresholds for the lightness pattern were as high as 25% —ie there was a large (about a log unit) contrast range where the edge was visible, its polarity was correctly identified, but there was no lightness difference between the two sides of the edge. At higher spatial frequencies, the masking pattern was equal for the two masking conditions. The results show that feature detection and identification is not a sufficient requirement for the emergence of the lightness pattern. We suggest a specific role of low spatial frequencies in lightness perception.

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◆ **Bi-dimensionality of achromatic colours as derived from multi-dimensional scaling**

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A multi-dimensional scaling (MDS) technique was used to study achromatic colour of Munsell chips under different illumination. Observers were presented with two sets of seven chips. The illumination of each set was independently set at one of three levels, maximal luminance (of white) being 417 , 133 , and 47 cd m^{-2} . The task was to evaluate the dissimilarity between pairs of chips on a 30-point scale. A matrix of dissimilarities, averaged across all observers and presentations, was used as an input into a non-metric MDS algorithm. The output was a two-dimensional fan-like pattern with three parallel arcs and seven converging radii (of three points each). Chips with the

same reflectance lie along the same radius. Chips with the same illumination lie along the same arc. Chips lying along the same radius are ordered with respect to their illumination. The points on each radius are ordered with respect to reflectance. After rotation by approximately 45° the axes may be interpreted as perceptual dimensions correlated with (i) lightness, and (ii) what D Katz called 'pronouncedness'—we prefer 'apparent illumination' (though not brightness of reflected light). The arc length (ie lightness scale) was found to contract when illumination decreased. This is in line with an intuitive view that in the limit (in darkness) it will shrink into a point. Thus, lightness scale was found to be different for different illuminations. For instance, when illumination increases, the black became blacker and the white whiter. Hence, lightness and apparent illumination are not independent dimensions. Instead, achromatic colours constitute an essentially two-dimensional manifold that cannot be factored into two one-dimensional continua of lightness and apparent illumination.

◆ **Illumination-independent lightness constancy improves also when the ratio invariant is violated**

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The visual system contends with two types of constancy. The first is in respect to change in the illumination (illumination independent), the second is in respect to change of the background (background independent). The tendency toward one of these types of constancy weakens the other type. In a CRT experiment we put two patches on two adjacent backgrounds (immediate backgrounds, IBs) that were both lighter than the patches. The two backgrounds lay, respectively, on two other different adjacent backgrounds (remote backgrounds, RBs). Two factors were systematically manipulated: (i) the luminance ratio between IBs and RBs, and (ii) the luminance ratio between the two RBs. Observers were asked to adjust the luminance of one patch to equate the lightness of the other. Two main results emerged: (1) Both types of constancy increase when the luminance ratio between the two RBs is larger than the luminance ratio between the two IBs (the first type when the ratio is coherent, the second type when the ratio is incoherent); (2) first type of constancy improves when IB is lighter than the RB. The opposite occurs for the second type of constancy. Our results show that lightness depends on: (a) the luminance ratio between the target and IB; (b) the luminance ratio between the two RBs; and (c) the luminance ratio between IB and RB. Therefore, these results strongly support an edge-integration mechanism, rather than local-contrast theories. Furthermore, in addition to the Gilchrist notion of ratio invariance (1988 *Perception & Psychophysics* **43** 415–424), illumination-independent lightness constancy can be enhanced even when the ratio at the intersection between an illumination and a reflectance edge is not invariant.

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◆ **Scene geometry and perceived lightness of real objects: Parametric measurements and models**

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When a planar object is rotated with respect to a directional light source, the luminance reflected to an observer changes. Thus, to achieve lightness constancy, the visual system must incorporate scene geometry into its calculation of surface lightness. We are interested in understanding the extent to which it does so. Here we report parametric measurements of how lightness matches depend on the reflectance and pose of an object. On each trial, observers viewed a directionally illuminated standard object and indicated a match from a palette of 36 grey-scale samples. The standard objects were uniformly painted flat cards (8 reflectances) displayed in one of 5 orientations. Each reflectance/orientation was randomly displayed once during a session (3 sessions per observer). Two groups of seven observers each performed the same matching task but under different instructions. One group was instructed to 'match the appearance' of the standard; the other to 'match the reflectance'. For each observer and reflectance, match-versus-orientation functions (MvO) can be established; averaged and normalised to provide an overall MvO function that for a lightness-constant observer should be flat. For an observer matching luminance, the MvO will have the same shape as function relating card luminance to orientation (LvO). Some observers in the 'appearance-match' group had MvO curves quite similar to the LvO curves. No observers had flat MvO curves, although some observers in the 'reflectance-match' condition had MvO curves that could be described as flat over a range of luminances. The data should support parametric modelling efforts that describe how lightness varies with object pose, and we plan to report on our modelling efforts as well as our data.

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◆ **Scene geometry and perceived lightness of real objects: Effects of instructions**

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In a previous study (Ripamonti et al, 2003 VSS 03, Abstract 89) we investigated lightness constancy for planar objects viewed in two different poses with respect to the light source. Observers were instructed to choose a sample on a palette whose reflectance matched that of the standard. We found significant individual differences, ranging from complete lightness constancy to no constancy. In the present study, we explored whether individual differences resulted because different observers interpreted the instructions differently. Two groups of seven naïve observers each performed the same matching task but under different instructions. One group was instructed to “match the appearance” of the standard (‘appearance-match’ group); the other was instructed as in our previous experiments (‘reflectance-match’ group). On each trial, observers viewed a standard object and indicated the best match from a palette of 36 gray-scale samples, both located in an experimental chamber illuminated from above by a theatre stage lamp. The standard objects were uniformly painted flat cards with 8 different standard reflectances, each displayed in the same 2 orientations as in the previous study. By comparing observers’ matches with the change in luminance across the orientations, we were able to compute a constancy index (CI) for each observer; CI = 1 indicates perfect constancy, CI = 0 indicates no constancy (luminance match). Mean CI for the ‘appearance-match’ group was 0.39 [−0.60 to 0.98]. Mean CI for the ‘reflectance-match’ group was 0.82 [0.2 to 1.15] which was not significantly different from previous study. The inter-observer variability remained large for both conditions, and the mean CI difference between the two groups was not significant. Varying the instructions provided to observers seems to result in a different matching behaviour, although more experimental work will be required to verify this conclusion. This result suggests that observers have access to multiple strategies for setting lightness matches under our stimulus conditions.

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◆ **The role of luminance ramps in lightness**

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Many delightful illusions have been produced with displays that contain luminance ramps (shallow gradients). Several theoretical accounts have been given for the role of luminance ramps in lightness. Luminance ramps influence lightness because they serve as a cue to the illumination (Helmholtz), their amplitude is underestimated (McCann), or they determine edge classification (Gilchrist, Bergstrom). A different role has been proposed by anchoring theory: luminance ramps serve to insulate frameworks from each other, preventing anchoring influences across the ramp. We report experiments in which this insulation hypothesis predicts a counterintuitive result, opposite in direction to that predicted by all the alternative theories. A homogeneous disk of light was projected onto a large rectangular black paper mounted on a wall. Several additional paper squares were added to the display to increase articulation, both within the spotlight, and outside it. In two conditions, the boundary of the spotlight was either sharp or blurred. According to the insulation hypothesis, blurring the disk boundary should insulate the region within the disk, creating a separate framework within which the highest luminance should rise towards white, pulling darker regions with it. Thus, regions within the disk should appear lighter (ie less constancy) when the disk boundary is blurred than when it is sharp. All the other theories predict the opposite result: darker values (and greater constancy) when the boundary is blurred. We found that target regions within the blurred contour were seen as significantly lighter than those within the sharp boundary. This supports the hypothesis that luminance ramps function to insulate perceptual frameworks from each other.

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FRIDAY
ORAL PRESENTATIONS**ATTENTION AND AWARENESS**◆ **Context-related facilitation in object recognition depends on spatial attention**

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Most current theories of object recognition implicitly assume the selection of one object at a time, and function poorly if given input from multiple objects. We tested this assumption by combining object naming with a task designed to manipulate the spread of attention to include the target alone (narrow focus) or the target with distractors (wide focus). The best observed performance (error rates) in the naming task was attained when attention was narrowly focused with no distractors present. The inclusion of any distractors in this condition resulted in significant performance deterioration. When attention was widely focused to include distractors, performance suffered little if distractors were semantically related to the target. The wide focus did impair performance if it included semantically unrelated distractors or no distractors (both showed significantly higher error rates). This experiment demonstrates that even a simple context, made up of separate objects rather than a coherent scene, can influence object recognition. The effect arises even though target and context are presented very briefly (80 ms) and masked, and the target can be located without searching. It also illustrates that the application of spatial attention to context, as well as the semantic relatedness of the context, is important for contextual facilitation. However, this experiment does not indicate whether the context is affecting early perceptual processes or later decision processes.

◆ **Attentional effects on sensory tuning for single-feature detection and double-feature conjunction**

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The purpose of this study was to explore the role of attention in binding different perceptual attributes, such as orientation and colour. Stimuli consisted of 8 peripheral patches symmetrically arranged around fixation; each patch contained a set of segments, and each segment took a random orientation and colour. One of the 8 patches (the target) contained an extra number of elements that were (in 3 separate experiments) either all vertical, all blue, or both. On each trial, subjects were either cued to the target patch and to the patch on the opposite side of fixation (2AFC), or were not cued and had to pick the target out of all the 8 patches (8AFC). Psychophysical reverse correlation was then used to derive tuning functions to orientation only, colour only, and to the conjunction of the two, in the presence and in the absence of attention (cued versus uncued). Attention had no effect on detection of single features—orientation (and colour) tuning in cued and uncued conditions was very similar. However, attention broadens tuning to the conjunction of these two features. It is concluded that tuning functions for single-feature detection are unaffected by attention, in line with the physiological literature. However, attention is associated with detuning of the filters operating conjunction of two features. This detuning is not accompanied by a decrease in task performance, which is the same for cued and uncued conditions. Possible interpretations of this discrepancy (eg internal noise) are discussed.

◆ **On the role of attention in the processing of transparent motion**

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The simultaneous perception of several motion directions—motion transparency—can be demonstrated with random-dot kinematograms in which groups of randomly distributed dots move in different directions within the same region of the visual field. In a computational approach, we demonstrate that a simple 2-D motion-detector network (2-DMD) would be able to separate a considerable number of motion directions that are presented within the same region which corresponds to the minimum separable direction difference of two overlapping groups of moving dots. Whereas the 2-DMD model predicts the perceptual limits for separating two different transparent directions rather accurately, model performance goes far beyond that of human observers who can discriminate no more than 2–3 superimposed directions from a random distribution of directions when other cues from which to discriminate the groups of dots (eg depth, colour) are excluded. This pattern of similarities and discrepancies between simulations and psychophysical results suggests that there is a bottleneck in motion-information processing, possibly related to visual attention. We studied experimentally the role attention

plays in separating transparent motion. When observers receive a cue to attend to a particular motion direction, it is possible to detect this direction in the presence of up to 6–8 superimposed directions; but observers fail to extract a particular direction from the combined flow of dots if the target direction is unknown. Thus, attention here appears to be attached to a particular feature—motion direction—rather than to a specific location and it can be utilised to retrieve information which is encoded in the early visual system but not explicitly available to an inattentive observer.

◆ **Morphing and object-based attention**

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Attention can be directed to a spatial region or to an object. The latter is demonstrated when two objects appear side by side, and attention can move more quickly from a cue at one end of one of the objects to a target at the other end than from a cue at one end of an object to a target in the other object, the same distance away. We tested whether changing the identity of the object between the appearance of cue and target will disrupt the object-based attention effect. The results show that when a morph intercedes, the time to move from cue to target shows an effect of distance more in line with space-based attention than object-based attention. These results are compared to a condition where the object moves but does not morph between cue and target. We conclude that a change in structure too big to be interpreted as a plausible distortion of an object causes attention to be redirected to the object. Identity continuity is important to object constancy.

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◆ **Independent attentional resources for vision and audition**

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Our aim was to determine whether vision and audition share common or independent attentional resources. First, psychometric functions were calculated to determine baseline performance for a primary task in each sensory modality. In vision, observers judged which of two lateralised grating patches had higher contrast; and in audition, which of two lateralised tones had higher pitch. Second, psychometric functions were calculated for a 'distractor' task. In vision, observers judged whether one element in a brief array of dots was brighter than the others; and in audition, whether a brief triad of tones formed a major or a minor chord. Then, in a divided-attention paradigm, psychometric functions were recalculated for the primary tasks while the distractor tasks were being carried out simultaneously. These divided-attention conditions were either intramodal (Vis–Vis, or Aud–Aud) or extramodal (Vis–Aud, or Aud–Vis). Task difficulty in the secondary task was fixed at threshold level. Discrimination thresholds for the primary task were found to be the same in the dual-task condition and the single-task baseline condition provided the distractor task was extramodal. This was true for both auditory and for visual primary tasks. In contrast, primary-task performance was much worse—by a factor of about 2–3—if the distractor task was intramodal. This effect was largely independent of the level of difficulty in the distractor task. The results demonstrate no 'cost' involved in doing two tasks simultaneously, provided they are in separate sensory modalities, regardless of the difficulty of the second task. In contrast to other claims, this strongly suggests independent attentional resources for audition and vision.

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◆ **Serial or parallel attention? A classification movie study**

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A central debate in the study of visual attention is whether attention is deployed in a serial or parallel manner. Response times in visual search have been explained by the serial allocation of visual attention, while human performance in visual search accuracy studies is typically accounted by a parallel deployment of attention with noisy processing of the visual information. Here, we examine the temporal deployment of visual attention by using the classification movie technique, a temporal extension of the classification image technique, to estimate how observers temporally weight the visual information at two cued locations. Observers searched for a Gaussian contrast increment target that appeared in 50% of the trials within two randomly simultaneously

cued locations among eight possible dimmer Gaussian pedestals (display duration = 200 ms). The contrast of the target and distractors was randomly varied every 25 ms. The sequence of noise samples appearing at the two cued locations in false-alarm trials was used to estimate the temporal weighting of the visual information at the cued locations used by the observers to make their decision. If attention is systematically serial, then the temporal weights for the two cued locations should not be simultaneously different from zero on the same temporal interval. Our classification movies show temporal weights larger than zero for the two cued locations at the same temporal interval. Therefore, our results suggest that observers are simultaneously using information at both cued locations at a given temporal interval consistent with the parallel deployment of visual attention.

◆ **Toward a general model of the spatial distribution of visual attention**

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The constraints on the spatial distribution of attention are investigated in a search task that requires observers to attend to more than one location, with a high penalty for attention to intervening areas. Several task variations are then used to develop a general model of spatial visual attention. In the search task, to-be-attended areas are parallel stripes organised in a square-wave grating pattern. One target is located on one of the even stripes, and ten false targets (identical to the real target) are located on odd stripes. Observers report the row and column of the target. As the spatial frequency (number of to-be-attended stripes) of the grating increases, performance decreases. In the model, an input stimulus (a search array) is processed successively by a spatial acuity function, a 'low-pass' spatial-attention filter, and a decision stage that combines bottom-up and top-down information. Each stage contributes to the item strength at each location to produce a final-strength map. The location with the highest strength is selected as the target location. This model generated predictions of performance on a trial-by-trial basis for three observers, 1440 individual predictions per observer. Model predictions correspond with observers' performance on an average of 70% of trials. Two observers repeating a total of 2016 identical trials made the same response on 76% of trials. The model both gives an accurate account of the data and characterises the limits of spatial attention. In principle, the model applies to any requested distribution of spatial attention.

◆ **Attention-driven conscious bi-stable stereoscopic depth perception**

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Voluntary control in conscious perception was studied by exposing the visual system to a novel ambiguous depth stimulus. Observers estimated the orientation of a grid in 3-D space. Monocularly and binocularly specified grid orientations were independently varied across stimulus presentations. Observers perceived only one orientation when the two specified orientations had the same sign. More interestingly, observers were able to select either a monocularly or a binocularly dominated percept when the two specified orientations had opposite signs (van Ee et al, 2002 *Journal of Vision* 2 597–607; *Journal of the Optical Society of America* in press; VSS03). Moreover, observers were able to flip at will between the two percepts in a relatively well-controlled way, implying that conscious vision can be studied physiologically (by neurophysiology, fMRI) in a well-controlled way. To understand the underlying mechanisms here, it is suggested that (i) in quite a few subjects the increase in percept-dominance duration due to voluntary control is large (as compared to the classical binocular rivalry stimuli); (ii) eye movements and blinks do not correlate with the perceptual flips; (iii) a Bayesian cue-integration model explains the data.

◆ **Orientation information of unresolvable Gabor patches primes ambiguous motion but not serial search**

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It has been demonstrated that in a choice between movement along lines drawn parallel or orthogonal to possible motion paths, observers more often see movement along the lines parallel to the motion path. Lines indicating the path of movement can generate the perception of a biased bistable apparent motion direction and disambiguate bistable motion display (Francis and Kim, 1999 *Perception* 28 1243–1255). In the first experiment, it was shown that orientation information of Gabor patches whose spatial frequencies were beyond the perceptual resolution limit (unresolvable) could perceptually prime a specific direction in a bistable motion paradigm even better than that of resolvable Gabor patches. In the second experiment, an orientation array with either resolvable or unresolvable oriented items was presented before a serial search task.

The target of serial search task at the location of unresolvable singleton (unique item) in the orientation array was not primed as well as the target at the location of resolvable singleton, implying that no orientation-dependent interactions were observed when several unresolvable Gabor patches were placed in close proximity. The results suggest that, although orientation signals are registered at least at the earliest stages of cortical processing without necessarily being consciously perceived, yet the processing of orientation difference and contextual modulation of orientation signals could not happen in such a perceptually unresolvable condition.

[The author wishes to thank Patrick Cavanagh for insightful comments.]

LOW-LEVEL PROCESSES

◆ A biologically plausible gradient-based model for robust measures of spatial orientation

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Spatial orientation is a fundamental low-level measurement in human vision that indicates how image structure is aligned in space. A gradient-based approach successfully applied in previous work modelling motion perception has been used to develop and implement a robust computational model to measure local spatial orientation. The model combines results from a series of steered (rotated) Gaussian-differential filters of increasing order applied at each point in image space. The derivative operators are applied around a succession of equally spaced 'principal' orientations at the stimulus point in question. These oriented derivative operators model the orientation-selective properties of the orientation columns in primary visual cortex. At each principal angle we also measure the corresponding orthogonal derivatives. The 'principal' and orthogonal differential measures are then combined to form a robust quotient (tangent) measure for each of the principal orientation angles. Local stimulus orientation is finally recovered by examining the phase shift, relative to a fixed frame, of the distribution of quotients over the set of 'principal' direction angles sampled. Initial results from simple visual stimuli such as sinusoidal gratings show good performance in recovering the orientation of local image structure at all points in the image. The model gives insight into the cause of misperceived orientation when applied to geometric optical illusions such as the Café Wall.

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◆ Perceiving edge blur: Gaussian-derivative filtering and a rectifying nonlinearity

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A template model for edge perception successfully predicts perceived blur for a wide variety of edge profiles (Georgeson, 2001 *Journal of Vision* 1 438a). The model differentiates the luminance profile, half-wave rectifies this first derivative, and then differentiates again to create the 'signature' of the edge. The spatial scale of the signature is evaluated by filtering with a set of Gaussian derivative operators whose response measures the correlation between the signature and the operator kernel. These kernels thus act as templates for the edge signature, and the position and scale of the best-fitting template indicate the position and blur of the edge. The rectifier accounts for a range of effects on perceived blur (Barbieri-Hesse and Georgeson, 2002 *Perception* 31 Supplement, 54). It also predicts that a blurred edge will look sharper when a luminance gradient of opposite sign is added to it. Experiment 1 used blur-matching to reveal a perceived sharpening that was close to the predicted amount. The model just described predicts that perceived blur will be independent of contrast, but experiment 2 showed that blurred edges appeared sharper at lower contrasts. This effect can be explained by subtracting a threshold value from the gradient profile before rectifying. At low contrasts, more of the gradient profile falls below threshold and its effective spatial scale shrinks in size, leading to perceived sharpening. As well as explaining the effect of contrast on blur, the threshold improves the model's account of the added-ramp effect (experiment 1).

◆ The effects of temporal adaptation on the perception of flicker duration

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We investigated whether temporal perception can be modified locally through adaptation to flicker. Subjects judged the durations of intervals containing 10 Hz sinusoidal modulation of spatially localised 2-D Gaussian profile luminance blobs (SD 1.15 deg). The adaptation stimulus was either 5 Hz or 20 Hz Gaussian flicker, centred 9.2 deg to the left or right of fixation.

The first of a run of trials was preceded by 30 s, and subsequent trials by 5 s, of adaptation. Adaptation was followed by two consecutive test intervals with test stimuli being shown on both the adapted and unadapted side. The order of presentation was randomised. Subjects reported which of the two appeared to last longer. The duration of the tests presented on the adapted side was fixed (250, 500, or 750 ms). The duration of the tests presented on the unadapted side was varied systematically (standard duration $\pm 60\%$) to measure a psychometric function. The point of subjective equality provided a measure of perceived duration after adaptation. We found that perceived duration decreased after 20 Hz and increased after 5 Hz adaptation. The reduced apparent duration was accompanied by a reduction in the apparent number of cycles. We propose that there are spatially distributed local mechanisms for visual time perception and that duration perception for dynamic visual pattern is mediated by these mechanisms whose characteristics are altered by temporal-frequency adaptation.

◆ **Flanked targets: easier to see, harder to identify**

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Crowding refers to the difficult identification of peripherally viewed targets amidst similar stimuli. Flanking facilitation refers to the easy detection of an oriented target when it appears amidst collinear stimuli in the centre of the visual field. These two well-documented effects seem difficult to reconcile within any unified framework for visual detection and identification. To quantify these effects, we measured the accuracy with which observers could discriminate between clockwise and anticlockwise tilts and the contrast required for detection of nearly horizontal targets in the presence and absence of horizontal flanks and spatially coincident pedestals. The effect of flanks upon identification accuracy was much greater than the effect of a pedestal that similarly lowered detection threshold. It was even greater than would be predicted if estimates of target and flank orientations were averaged prior to identification. A single population of orientationally selective filters can simultaneously produce identification accuracies and detection thresholds similar to those we measured with and without spatially coincident pedestals, but not those we measured using spatially separate flanks. Previously, we have proposed a filter–rectify–filter model of flanking facilitation. A population of these second-order filters can simultaneously produce thresholds similar to those we measured using flanks.

◆ **Artificial scotomata: ‘filling in’ and/or masking?**

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Peripherally viewed, zero-contrast ‘holes’ in dynamic random noise completely disappear during prolonged fixation. Is this due to filling in (ie noise perceived in the hole) or masking (ie sensitivity decrement in the ‘hole’ detector)? We used a spatial 2AFC paradigm to measure thresholds for detecting brief (100 ms) flashes of noise in artificial scotomata. Thresholds increased monotonically with the contrast of the background noise. We also measured thresholds for detecting increments in the contrast of noise flashes on zero-contrast pedestals. These thresholds formed a dipper-shaped function of pedestal contrast. Together, these two results argue against a filling-in theory of contrast-boundary disappearance. Masking theory can account for these results, but there is another phenomenon which cannot be explained in the same way. When the noise background contrast is replaced by mean luminance, observers have the fleeting impression of noise where the holes had been (Ramachandran and Gregory, 1991 *Nature* **350** 699–702). We measured thresholds for detecting real noise in the same position as these phantasms. Although the contrast of the adapting stimulus (ie the background noise) appeared to have a large effect on the contrast of the phantasms (when mean luminance was not co-varied), it had only a slight effect on threshold for detecting real noise in the same location. All of our results are consistent with a second-order opponent mechanism for noise boundary detection, whose sensitivity can be attenuated by adaptation.

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- ◆ **Human cortical responses to visual features: An fMRI validation of the local-energy model**
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Visual features, such as lines and edges, carry much information about both the details and the perceptual organisation of images. The local-energy model of feature detection (Morrone and Burr, 1988 *Proceedings of the Royal Society of London, Series B* **235** 221–245) has proven successful in segmenting and predicting perceptual appearance of visual scenes (real and illusory) on the basis of salient features. The model comprises a first stage that localises in space all features by local maxima of local-energy functions, and a second stage that identifies the type of feature by evaluating phase information at these maxima. We tested the biological validity of the local-energy model, studying the human brain BOLD response to stimuli with identical power but different phase spectra: a structured image comprising pure edges or pure lines and noise stimuli with random phase. Stimuli with pure lines and edges have identical local-energy functions at all scales, even though the Michelson contrast of these stimuli differs by a factor of four. The random stimuli have completely different local-energy functions and about half of the Michelson contrast of edges. Alternation of lines or edges stimuli against the random stimulus produced a strong activity in primary visual cortices (V1/V2) in all eight subjects, as well as activity in an associative cortex of BA19 (average Talairach coordinates $-38, -90, 8$). However, alternation between stimuli with the same local energy (lines versus edges) produced no activity in primary visual cortex, but did elicit strong activity in BA19 in all subjects. These data suggest that primary visual cortex could compute stimulus local energy, while BA19 may be responsible for classification of image type on the basis of local phase information.
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- ◆ **What defines a contour in metacontrast masking?**

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Metacontrast masking occurs when a target stimulus is followed after a short stimulus onset asynchrony (SOA) by a mask that shares a contour with the target (Breitmeyer and Ogmen, 2000 *Perception & Psychophysics* **62** 1572–1595) and leads to a reduction in perceived brightness and to degraded perception of the spatial shape of the target. It is believed to depend strongly on the spatial overlap of target and mask contours (Macknick et al, 2000 *Proceedings of the National Academy of Sciences of the USA* **97** 7556–7560). Here, we present a new form of backward masking which shares many features with metacontrast masking but does not rely on shared contours. Targets and masks were horizontal high-luminance square-wave gratings with a 5% duty cycle (parallel lines). Targets were presented at fixation, and masks were presented immediately adjacent to the left and right of the targets. Subjects judged the perceived brightness of the targets while we varied the SOA and relative spatial phase between targets and masks. With this geometry, targets and masks did not share a classical luminance-gradient contour, especially when targets and masks were spatially in antiphase. Nonetheless, we found a biphasic modulation of perceived brightness. At SOAs below -200 ms and above 300 ms masked targets were judged to have the same perceived brightness as single targets. At SOAs around -100 ms to 0 ms target brightness was perceived to be enhanced, whereas around 0 ms to 300 ms it was perceived to be reduced, as in metacontrast masking. Strikingly, the relative spatial phase between target and mask had no influence on the masking function. Implications of the results for neurophysiological models of metacontrast masking, object substitution masking, and spatial pooling are discussed.

- ◆ **The loss of area summation in contrast masking is a ‘within-channel’ effect**

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At detection threshold, sensitivity improves with the area of a test grating, but not when it is placed on a pedestal. This raises two questions about area summation: (1) Is it specific to within-channel masking? (2) Can it be explained by lateral suppression from the pedestal? To address these issues we measured masking functions for six conditions. Within-channel masks (pedestals) and test gratings were vertical, and cross-channel masks were horizontal (for example). For both configurations, the test and mask could be both small (SS), both large (LL) or small, and large, respectively (SL). For within-channel masking, area summation was found in a ‘dipper’ region and masking was slightly greater for SL than SS. However, for cross-channel masking, results for

SS and SL were identical and those for LL were transposed downwards on a log-axis, indicating area summation across the entire function. In a standard model of masking, the weights of excitatory and suppressive terms were allowed to vary across the three size conditions. Acceptable fits were found when: (a) the weight of the excitatory contrast term (test + pedestal) increased with the size of the test, (b) the weight of lateral suppression from the pedestal was constant, and (c) the weight of the divisive cross-channel mask did not depend on the size of the mask. We conclude that: (i) there is no lateral suppression for cross-channel masks, (ii) there is lateral suppression from large pedestals, (iii) the loss of area summation above threshold is a property of within-channel masking, and (iv) reducing the size of a grating stimulus affects within-channel and cross-channel masking in a similar way to contrast adaptation (eg Meese and Holmes, 2002 *Vision Research* 42 1113–1125).

◆ **The dichoptic standing wave of invisibility: Implications for awareness and models of visual masking that require feedback or cortical circuits**

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Most models of visual masking require cortical circuits to play a role because dichoptic forms of visual masking exist and therefore seem to implicate binocular circuits found only in the cortex. However, we and others have shown that monoptic forms of physiological visual masking effects occur subcortically. To explain these subcortical masking results, it has been suggested that there may be an underlying cortical mechanism that is then fed back to the lateral geniculate nucleus (LGN). To test this idea, we recorded from neurons in the awake macaque LGN, as well as in monocular and binocular neurons of area V1, while stimulating with dichoptic and monoptic forms of visual masking (the standing wave of invisibility). Neural responses to the target were suppressed in the LGN and in area V1 when the masks and targets were presented to the same eye. However, in all monocular cells tested, responses to the target were unaffected when targets were presented to one eye and masks were presented to the other eye (dichoptic masking condition). Neither interocular transfer of inhibition nor binocular inhibitory feedback was therefore found in monocular cells of the early visual system, suggesting that feedback from dichoptic levels of processing does not account for monoptic masking in the early visual system. We propose a simple model of masking based on lateral inhibition: a circuit that is known to exist at all levels of the visual system where it has been looked for. Lateral inhibition can account for most, if not all, masking effects, including ‘object substitution’, which has thus far been explained with models involving high-level cognitive processes. We, moreover, conclude that neural responses within monocular cells are not sufficient to generate target visibility.

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TOP–DOWN, BOTTOM–UP, AND SIDEWAYS INTERACTIONS‡

- ◆ **Top – down, bottom – up, and sideways in infants’ development of visual object organisation**
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The ability to assign an image region as an object, segmented from its background, is important in the development of visual processing, requiring bottom–up stimulus information, ‘sideways’ interaction between concurrent processes, and top–down attentional selection by top–down processes. We discuss our experimental evidence in several diverse areas, on infants’ ability to assign ‘object-ness’ and its implications for different levels of processing: (a) Image segmentation, on the basis of either motion and form properties, can guide infants’ preferences. However, early-developing orientation processing is weaker in determining preference than later-developing motion processing, perhaps reflecting greater reliability of motion cues for object assignment. (b) Figure–ground assignment is essential in defining object shape—requiring a ‘sideways’ interaction between representations of contours and background regions. We review current experiments, on differential sensitivity to properties of figure and ground regions in infants aged 2–4 months. (c) Visually goal-directed actions, in particular reaching and grasping, require object assignment followed by target selection. Infants must distinguish between localised, cohesive objects and regions representing extended surfaces (eg walls). We have used the ELITE motion-analysis system to analyse uni-manual and bi-manual reaching and grasping by infants aged 6–9 months, to gauge the parameters controlling identification of a region as a target for specific action patterns. Data from these paradigms allow identification of bottom–up processing

‡ In honour of Richard Gregory.

of stimulus information, with differential levels of modulation by parallel and top–down selection for object assignment, at different stages of infant development; a starting point for developmental neurobiological models of these interactions.

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◆ **Top – down knowledge affects the perception of inside-out objects**

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Gregory [1970 *The Intelligent Eye* (Weidenfeld and Nicolson, London)] explained the well-known hollow-head illusion in terms of top–down knowledge of normal convex faces. This has been questioned by Hill and Bruce (1993 *Perception* **22** 887–897) who suggested that, rather than specific object knowledge, there is a general tendency to see objects as convex. We have found that inside-out ears do not look convex, but flip to look concave supporting Gregory's explanation. Experiments are reported in which the perception of inside-out and normal faces, potatoes, ears, and geometric shapes has been compared under two conditions of lighting.

◆ **Depth and distance scaling under telestereoscopic viewing: The roles of vergence and differential perspective**

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Increasing the interocular distance (IOD) under telestereoscopic viewing modifies the disparities of all objects in the visual scene by a factor of $IOD_{\text{telestereoscope}}/IOD_{\text{normal}}$, and so it is not surprising that the apparent depth of 3-D objects and surfaces increases. At the same time, the perceived distance of objects decreases, owing to the increased vergence. The aftereffects of perceived depth and absolute distance have been attributed to a recalibration of the vergence system. However, telestereoscopic viewing not only increases the required vergence of nearby objects, but also increases the amount of differential perspective (pattern of vertical disparities) which provides information about the absolute distances to objects in the scene. This raises the possibility that the changes in perceived depth and absolute distance with telestereoscopic viewing may be due to the changed pattern of vertical disparities rather than the increased vergence demand. To test this possibility, the extent of telestereoscopic viewing was manipulated, from a doubling of the interocular distance through to synoptic viewing (in which the IOD is reduced to zero), and the amount of perceived depth and surface curvature of 3-D objects was measured. The size of the visual field was also varied from < 10 deg diameter (which has been shown previously to be ineffective in depth and size scaling) up to 80 deg diameter. The results indicate that, whilst the changed vergence demand per se affects perceived depth and absolute distance, the changed differential perspective also plays a significant role, both in the perceived structure and layout of 3-D objects and in the recalibration of the vergence system.

◆ **Crossover motion and White's effect**

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When two vertical bars lying side by side, one light-grey and one dark-grey, suddenly exchanged luminances, apparent motion was seen in a direction that depended on the surround luminance. On a light surround the dark-grey bar appeared to jump, and on a dark surround the light-grey bar appeared to jump. Thus the bar with the higher contrast against the surround was seen as moving in a winner-take-all style. Next, the vertical bars were embedded in long vertical black lines, on a white surround (or vice versa). One might expect that a white surround, which abutted the long edges of the test bars, would affect their perceived lightness more than the embedding verticals, which only touched the tiny tips of the bars. But owing to White's effect (White, 1979 *Perception* **8** 413–416; 1981 *Perception* **10** 215–230) the embedding lines subjectively lightened the grey bars far more than the white surround darkened them. Consistent with this, a titration method showed that the black embedding lines were three times as important as the white surround in driving apparent motion. White embedding lines and a black surround gave the expected converse results. The conclusions are: (i) motion strength is determined by stimulus contrast; (ii) motion is computed after White's effect.

[Supported by a UCSD Senate grant.]

◆ **Leaves, fruit, shadows, and lighting in Kibale Forest, Uganda**

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There has been much debate about the links between primate colour vision and the properties of fruit and leaves eaten by trichromatic primates living in the wild. However, attempts to explore the spatio-chromatic properties of such stimuli are more recent. Párraga et al (2002 *Current Biology* **12** 483–487) showed a correspondence between the luminance and red–green Fourier spectra of images containing green leaves and red fruit, and the contrast sensitivity for luminance and red–green gratings, particularly at normal grasping distance. However, the fruit sampled in that study was growing in England, and not a tropical rainforest. Furthermore, the sample did not contain any red, unripe leaves of the type eaten by monkeys and also argued to be of importance for monkey vision (Dominy and Lucas, 2001 *Nature* **410** 363–365). We therefore obtained 223 images in Kibale Forest, Uganda, in the dry season of 2002. A further 80 images of two scenes, at intervals of 10–20 min, were also obtained to investigate changes in illumination. The images were obtained with a digital camera calibrated to output L, M, S cone responses for each pixel. The results are in keeping with those obtained earlier. Interestingly, there was no difference between images with red fruit and those with red leaves in this regard. The results are due to the strong invariance of the red–green opponent system to shadows. This extends, in the time-of-day images, to an invariance against natural changes in illumination allowing the relative colour of objects to be encoded in spite of substantial changes in the intensity and spectral content of the illuminant. The conclusion is that the red–green system has several important properties that make it fit for a variety of foraging operations.

◆ **Peiriodic Table of Illusions**

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Classifications are important in science, especially when related to theoretical concepts. Gaps in understanding may be revealed, and new experiments suggested. Here phenomena of perception, especially visual illusions, are classified by kinds and supposed causes, in a 'Peiriodic Table of the Elements of Illusions'. This is based on a Helmholtzian model of perception, where 'physiological' and 'cognitive' effects are distinguished, recognising of course that cognition depends on physiology for carrying out its processes. Classification demands explicit criteria (not yet fully worked out) for distinguishing kinds of phenomena and kinds of causes, which should clarify technical discussions and reduce ambiguities of interpretations. 'Ambiguity' itself turns out to be ambiguous: generally meaning either passive confusions or active generation of alternatives. These are extremely different, though often confused. They are named 'confounding' and 'flipping' phenomena of perception.

LIGHTNESS, BRIGHTNESS, SHADING, TRANSPARENCY 2

◆ **Why is the Benary effect so small?**

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Benary [1924 *Psychologische Forschung* **5** 131–142; translated into English in *A Source Book of Gestalt Psychology* Ed. W D Ellis (1939, London: Routledge & Kegan Paul)] was the first to systematically show that simultaneous lightness contrast (SLC) can be observed also when the local conditions at the target edges are identical. In his famous configuration, two identical gray triangles were placed one between two arms of a black cross and the other on the top of a big black triangle. The overall background was white. Therefore, they were locally bordering with the same amount of black and white area. Nevertheless, the gray triangle between the arms of the cross was perceived darker than the other triangle. Benary explained the effect according to the belongingness principle. It must be noted, however, that the effect is smaller than that observed in the classical SLC display. Recently, Agostini and Galmonte (1999 *Perception & Psychophysics* **61** 1345–1355) showed that contrast induced by belongingness is not an all-or-nothing process. To investigate whether the lightness of the two targets is influenced by the colour of the non-belonging bordering regions, in the present work we measured the Benary effect separately. A Munsell scale was placed on a white background. The two halves of the Benary configuration were measured separately under Gelb lighting. Observers were asked to choose from the scale the patch matching the target in lightness. Since the scale was on a white

background, the target belonging to the white background should be matched with its veridical value, while the target belonging to the black area should be matched with a lighter value. Surprisingly, both targets were matched with a lighter value, even though the amount of the induction was larger for the target included in the black area. Our experiments show that the colour of the non-belonging bordering regions in the Benary configuration has a detectable effect on the lightness of the target patch.

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◆ **The role of local luminance effects in lightness revisited**

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It is generally believed that lightness depends on luminance interactions between adjacent regions. However, several illusions in the literature seem to contradict this idea. One example is the Staircase Gelb effect in which 5 adjacent coplanar squares, ranging from white to black, are suspended in midair and specially illuminated. Observers perceive a range from white to mid-gray. What produces this compression? According to one explanation, the illusion is partially caused by each square being seen in relation to a standard referent, the white square. This 'anchoring' effect occurs irrespective of the adjacency of the referent to each square in the display. We tested this proposal in a series of experiments. In experiment 1, the squares in the display were systematically re-arranged. In experiment 2, two squares of equal luminance were placed next to different-luminance squares. If adjacency is important, then we can expect that in experiment 1 the lightness of the squares will change, depending on the luminance of their adjacent neighbours. In experiment 2, we can expect that the equal-luminance targets will appear different in lightness because of their different luminance neighbours. In experiment 1, the lightness of the squares varied with changes in their local-luminance ratios. In experiment 2, the equal-luminance targets looked significantly different when placed next to different-luminance squares. These findings suggest that, in addition to anchoring, adjacency also plays a role in the Staircase Gelb illusion. We discuss our results with respect to several theories.

[We would like to thank NEC Laboratories America for their support with this project.]

◆ **Systematic chromatic changes underlying colour transparency**

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Several studies (D'Zmura et al, 1997 *Perception* **26** 471–492; 2000 *Perception* **29** 911–926) have suggested that colour changes across a region of an image that can be described as translations and/or convergences in a linear trichromatic colour space lead to the perception of transparency, but other transformations, such as shear and rotation, do not. To study the limits of such systematic chromatic changes, we generated classes of stimuli including three additional categories defined as: equiluminant (vectors are in an equiluminant plane), filter (vectors point to a lower luminance), and illumination (vectors point to a higher luminance). Vector lengths were varied systematically, within the gamut of the CRT monitor. The stimuli consisted of a bipartite field partially overlaid by a square. Observers classified each stimulus according to whether the overlying square appeared transparent or not. The relation between the response variable and the stimulus categories was fit with a log–linear model and evaluated with the Pearson χ^2 statistic. The main results support the convergence model. However, large equiluminant translations were less often judged as transparent, consistent with observations reported by Chen and D'Zmura (1998 *Perception* **27** 595–608) with respect to colour changes that cross hue boundaries. Surprisingly, we found that small shears and divergences were also classified as transparent, in contradiction to the model. This could imply that two mechanisms underlie the perception of transparency: a low-contrast mechanism that is sensitive to chromatic and luminance change independent of its direction (translation, shear, convergence, or divergence), and one sensitive to higher contrasts that depends on the integrated direction.

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◆ **Neural mechanisms of achromatic colour perception: Filling-in, edge integration, and awareness**

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Many contemporary studies of lightness perception are guided by a basic theoretical model in which lightness, or achromatic colour, is computed in three stages involving: (i) neural encoding of local luminance ratios at the locations of luminance borders within the image; (ii) spatial

integration of these ratios to establish a scale of relative lightness values for the regions lying between borders; and (iii) anchoring of the relative lightness scale to a physical referent, commonly assumed to be the highest luminance in the scene. One important implication of this model is that the lightnesses of regions lying between borders are perceptually filled in by the brain. I present a neural theory of achromatic colour computation that is consistent with this scheme and show how it accounts for psychophysical lightness-matching judgments and for recent single-cell recordings from cortical area V1. A key assumption of the theory is that the spatial integration of local luminance ratios is computed by the simultaneous neural filling-in of achromatic colour signals originating from multiple luminance borders. Thus, the theory posits that filling-in serves to integrate edges. The theory is shown to be consistent with neural responses in V1 that develop 520–1220 ms after stimulus onset (Kinoshita and Komatsu, 2001 *Journal of Neurophysiology* **86** 2559–2570). The delayed response suggests an underlying mechanism involving feedback from higher cortical areas. Finally, I argue that the output of V1 undergoes a simple mathematical transformation at a subsequent stage of neural processing that maps it into a secondary signal having a quantitative form that matches that of the psychophysical lightness scale, and that V1 is therefore unlikely to be the cortical locus of achromatic colour awareness.

◆ **In search of neuronal correlates of ‘filling-in’: an fMRI study into brightness induction**

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Our visual system is known to ‘fill-in’ information that is physically absent. ‘Filling in’ occurs in many different ways. The blind spot is a well known example. The aim of this study was to find and locate the ‘filling-in’ neuronal correlates in the human visually healthy brain. The study focused on an illusion where a brightness change of a central disc is induced by a change in luminance of its surround. As the brightness change does not correspond with the stable physical nature of the central disc, it can be argued that the visual system ‘fills in’ these brightness changes. The experiment was conducted with the use of functional magnetic resonance imaging (fMRI). Eight healthy volunteers viewed a central disc and surround stimulus imaged on their fovea while their brains were scanned. The region of interest in the visual cortex, corresponding to the foveal region activated by the central disc, was delineated by a technique similar to retinotopic mapping. Brain activation in that specific region of interest was compared during two conditions: luminance change of the central disc and luminance change of the surround of the central disc while the luminance of the disc itself was kept constant. Preliminary results show similar increased brain activity in the region of interest during both conditions. Hence, we found activity in that region of visual cortex even though no physical changes were presented to the corresponding part of the retina. This suggests, first of all, that early visual cortex responses correlate with brightness changes. It further suggests that brightness ‘filling-in’ might take place at or prior to early visual cortex.

◆ **A cortical visual region within area 19 mediating the Cornsweet illusion**

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Some well-known illusory phenomena, such as the Cornsweet illusion, suggest that the perceived brightness of a surface is dictated by the local contrast at the contour. Here we measured the dependence of the Cornsweet illusion as a function of the contrast and of high-pass filtering of the image by brightness matching and fMRI, to determine whether specific areas of the human brain may mediate the illusory reconstruction of the surface brightness. Various versions of the Cornsweet stimuli were presented with added noise (randomly refreshed every 2 s to avoid adaptation), and the BOLD response was compared to that elicited by noise alone. This comparison revealed strong activation in primary visual cortex, but it was limited to the location of the border where the luminance actually changed: there was no activation to the ‘illusory brightness’. There was also a strong response in a region inside BA19. We then measured the response to the Cornsweet stimuli compared with stimuli perfectly balanced in local and global energy, but differing in phase spectra so as to eliminate the illusion. This produced no activation in V1, but the response of the region within BA19 remained strong. Furthermore, the fMRI response decreased at high contrasts, paralleling closely the psychophysical measurements of apparent brightness. Taken together, the results suggest that this region within area 19 may mediate the reconstruction of surface luminance from the edge contrast.

NATURAL IMAGES

◆ The influence of resolution on natural-image statistics

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Natural images are highly structured in their spatial configuration. Where one would expect a different spatial distribution for every image, as each image has a different spatial layout, we show that the spatial statistics of recorded images can be explained by a single process of sequential fragmentation. The observation of the fractal world by a resolution-limited sensory system deforms natural image statistics to the Weibull type distribution. The limited scale invariance of the observation by a retina of receptive fields, seemingly an artifact at first glance, turns out to have a profound influence on the statistics of natural images. Our experiments show that for the Corel general photo stock consisting of 46 695 images, 57% of the pictures conform to the theory of sequential fragmentation. For the van Hateren high-resolution and calibrated outdoor image collection, 82% of the images are significantly distributed according to the statistical process of fragmentation. This is a remarkable result, given the variety of generating processes for the pictures in the collections. The power-law and normal distribution represent the extreme cases of sequential fragmentation. Between these two extremes, spatial detail statistics deform from power-law to normal through the Weibull type distribution as receptive field size increases relative to image detail size. Hence, the fragmentation explanation of image statistics is much more important than the physical laws of fractals. Its perceptual significance follows from a comprehensive focus-of-attention mechanism.

[We acknowledge the discussion with Jan Koenderink and Sylvia Pont.]

◆ Temporal coherence and sparseness in the statistical structure of natural images

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Recent computational models attempt to explain how the classical receptive fields (CRFs) in V1 are related to the statistical structure of natural images. A seminal contribution proposed that simple-cell CRFs can be modelled as providing a maximally sparse code for natural images: any single natural image can be described by a limited number of active cells (Olshausen and Field 1996 *Nature* **381** 607–609). Recently, we proposed an alternative explanation based on the temporal structure of natural image sequences: simple-cell CRFs have maximum temporal coherence or stability over time (Hurri and Hyvarinen, 2003 *Neural Computation* **15** 663–691). Here, we present a model that combines these two seemingly unrelated principles, and shows how it is possible for them to lead to the same kind of CRFs. The model is based on modulating the amplitude of a Gaussian signal by a temporally correlated signal. This provides a better model of the outputs of Gabor filters in natural image sequences than either sparseness or temporal coherence alone. The model is further combined with a model of complex cells and topographic organisation (Hyvarinen and Hoyer, 2001 *Vision Research* **41** 2413–2423), thus providing a unifying framework for a number of models based on natural-image statistics. Intuitively, the model can be described as bubble-like activity patterns in the cortex.

◆ Attention on object events in video using recursive contextual cueing

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In computer vision, we face the challenging task of recognising objects of interest in outdoor environments. The presented work is based on psychological findings in human perception that highlight the utility of scene interpretation for contextual cueing of object events. Investigations on both scene recognition and object localisation provided clear evidence that local features play a decisive role to facilitate detection from predictive schemes (Hollingworth and Henderson, 2002 *Journal of Experimental Psychology: Human Perception and Performance* **28** 113–136). The visual system infers knowledge about stimuli occurring in certain locations leading to expectancies regarding the most probable target in the different locations. By analogy, we have modelled sensorimotor spatial attention by mapping landmark perception to attentive actions, ie guiding visual search along a most promising search direction. The original contribution of this work is to iteratively estimate attention from scene context by using knowledge about forthcoming detection events that has been automatically built up before. The simple scene model is matched with extracted landmark configurations to rapidly determine image regions where object detection events will most likely occur. The Bayesian prediction scheme enables recursive estimation of object locations from incoming evidence. The presented concept uses localised features that are rather invariant to scaling and translation. It proposes directive actions that guide perception

instead of binding them to absolute coordinates. In the experiments we demonstrate detection results from video and prove that landmark-based prediction of detection provides a highly efficient classifier under restricted use of resources.

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◆ **Visual determinants of eye movements revealed by reverse correlation**

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To determine the visual characteristics that specify where we move our eyes, we recorded saccades while viewing natural scenes. We then used the reverse correlation technique to determine the optimal (least squares) linear filter that operates on (potentially nonlinearly transformed) images to generate the observed saccades. This method has previously been used to identify visual, auditory, and tactile characteristics that determine spike generation in neurons. Here we attempt to predict saccaded-to locations. First, we constructed salience maps that made specific features of the images explicit: raw luminosity, difference of luminance from the mean, local contrast, chromaticity, and edge information based on the outputs of odd-symmetric Gabors. Each was performed at two spatial scales. We then measured saccade-triggered averages (STAs) for each of these salience maps. Unsurprisingly, no structure was found for the raw luminosity STA. For the other transformations, localised receptive fields were found at the high frequencies. STAs give some insight into the operation of the system, but a better characterisation is in terms of an optimal linear filter. The optimal filter is only equal to the STA if the inputs are uncorrelated, but this was not the case. To calculate the optimal filter with correlated inputs requires a matrix inversion of the input covariance matrix, which can be numerically unstable. We therefore used ridge regression with cross-validation to identify these filters stably. Most interestingly, edge information was weighted positively at high frequencies, but negatively at low frequencies. We interpret this as eye movements being determined partly by surface property boundaries whilst being invariant to gross illumination changes.

[We thank Iain Gilchrist for his help in the collection of the eye-movement data.]

◆ **Local boundary detection in natural images: Matching human and machine performance**

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Local boundary detection remains an important problem in vision. Physiology shows that V1 extracts complex boundaries (Lee et al, 1998 *Vision Research* **38** 2429–2454). Psychophysics shows that human subjects localise boundaries using multiple cues (Rivet and Cavanagh, 1996 *Vision Research* **36** 53–66). Our work in computer vision (Martin et al, 2002 *Neural Information Processing Systems* in press) shows how to formulate and combine local boundary cues in natural images. To determine the quality of computational models, we need a precise characterisation of human performance for the local boundary detection task. A large data set of ~ 1000 natural images (480×320 pixels), each segmented by about ten human observers, provides ground truth on-boundary/off-boundary pixel labels. We extracted 100 on-boundary and 100 off-boundary sample pixels, and presented radius $\{9, 18, 36\}$ patches centred at the samples to subjects in 200 ms exposures. The $r = 9$ patches subtended 0.85° . Subjects were asked if an object boundary passed through the patch centre. We also evaluated the machine model at each sample; its input is a radius 9 patch, and its output is the estimated probability of a boundary. We evaluated performance using precision-recall (PR) curves (similar to ROC curves) which can be summarised by the F -measure, the harmonic mean of precision, and recall. We find that the precision and recall of human subjects for radius 9 patches falls directly on the PR curve given by the machine boundary model, both with $F = 78\%$. Human performance increases with $r = \{18, 36\}$ patches to $F = \{83\%, 85\%\}$. The classification error is 21% for the machine detector, and $\{23\%, 18\%, 15\%\}$ for the human subjects at $r = \{9, 18, 36\}$. We conclude that the current state of the art in computational local-boundary detection on natural images matches human performance, and is therefore optimal by this measure.

◆ **Computer architecture for self-referential perceiving systems**

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An extensible architectural computer model for perceiving systems based on a knowledge-driven joint inference approach is presented. The model can integrate different sources of information both horizontally (multi-modal and temporal fusion) and vertically (bottom-up, top-down) through self-referential feedback and attentional control mechanisms. Self-referentialism arises through explicit representations of a system's internal state and goals expressed in terms

of an active knowledge-representation framework based on an extensible ontological language. It forms associations between sensory inputs and semantic structures and enables perceptual inference to consist of parsing queries posed in an extensible visual language incorporating prior hierarchical knowledge of the syntax and semantics of entities, relationships, and events of interest occurring in a given ontological domain. Implementations of the model are presented, including computer systems for content-based analysis and retrieval of digital image and video data. The model has also been applied to an embodied sensor fusion problem involving a sentient computer system deployed in a large office space. Sentient computing utilises sophisticated sensor infrastructures and world models to infer properties of the context within which human-computer interactions occur. Using the architectural model, different computer vision algorithms for tracking and recognition are fused with an ultrasonic location system to greatly augment the perceptual capabilities and robustness of both. It is shown how the framework enables adaptive fusion of different sources of information on the basis of an extensible ontological language in order to generate and integrate different hypotheses about the perceived context.

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FACE PERCEPTION

◆ Linking the structure and perception of 3-D faces: Sex, ethnicity, and expressive posture

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A statistical study of human face shape is reported whose overall goal was to identify and characterise salient components of facial structure for human perception and communicative behaviour. A large database of 3-D faces has been constructed and analysed for differences in ethnicity, sex, and posture. For each of more than 300 faces varying in race/ethnicity (Japanese versus Caucasian) and sex, nine postures (smiling, producing vowels, etc) were recorded. Principal components analysis (PCA) and linear discriminant analysis (LDA) were used to reduce the dimensionality of the data and to provide simple, yet reliable reconstruction of any face from components corresponding to the sex, ethnicity, and posture of the face. Thus, it appears that any face can be reconstructed from a small set of linear and intuitively salient components. Psychophysical tests confirmed that the shape is sufficient to estimate sex and ethnicity. Subjects were asked to judge the sex and ethnicity of (a) natural faces and (b) faces synthesised by randomly combining principal component coefficients within the database. Subjects successfully discriminated ethnicity and sex independently of posture, verifying that different combinations of components are required and in differing amounts. Finally, implications of these results for animation and face recognition are discussed, incorporating results of studies currently underway that examine the 'face print' residue of the sex-ethnicity factor analysis.

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◆ The facial information subtending the judgments of facial expressions

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There is little doubt that the categorisation of facial expressions is of great significance to humans as a species. From the seminal work of Ekman and Friesen [1975 *Unmasking the Face* (Englewood Cliffs, NJ: Prentice-Hall)] we know that faces display a limited number of basic emotions (happiness, surprise, fear, sadness, disgust, anger, and neutral), but we still do not know how facial features determine the perception of these expressions. Using the bubbles technique (Gosselin and Schyns, 2001 *Vision Research* **41** 2261-2271), we examined the determinants of the categorisation of each of these expressions, sampling information from a 3-D input space (2-D image \times 5 spatial scales) in 14 experimental conditions (7 expressions \times 2 genders). Two groups of observers (males and females) first learned to categorise the 7 expressions of five males and five females to 95% accuracy. During the experiment, they were exposed to facial information samples whose density was calibrated to maintain performance at 75% correct. Analyses of the use of information produced an effective stimulus for each gender-specific facial expression. In addition, ideal observers of the expression identification task, independently derived for male and female faces, provide benchmarks with which to compare the efficiency of the male and

female observers. These measures provide a rigorous account of how male and female observers differ in their judgments of facial expressions in male and female faces.

◆ **Effects of eye and face shape on perception of masculinity, attractiveness, and age**

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The effect of masculinity on male facial attractiveness has been studied with controversial results. Eye and eyebrows are sexually dimorphic and change when faces are warped along the male–female axis, but are also fundamental in decoding emotion. The effects of masculinity on attractiveness may be secondary to changes in the perceived emotional tone of the target stimulus faces. To dissect these two effects, we have created two sets of stimuli using conventional morphing techniques. In one set, the shape of eyes and eyebrows of an average male face was changed in a continuum along a morphometric male–female axis without warping the rest of the face. A second and complementary set of stimuli was created by warping face shape while blocking eyes and eyebrows. We asked twenty-five female observers to rate the four extremes of the two face continua for masculinity. It was found that either manipulation changed the perceived masculinity of the target face ($p < 0.01$). We then asked forty female observers to select the most attractive face along these continua as well as along a third continuum generated by warping eyes and face together. In accordance with previous reports (Perret et al, 1998 *Nature* **394** 884–887), female subjects showed a preference for slightly feminised male faces (–8% along the warp axis), when the whole face configuration was manipulated. When eyes and face outline were manipulated separately, a significantly larger degree of feminisation was preferred (–18% and –21%, respectively). We conclude that eyes and face outline contribute additively to the perception of masculinity, and that masculinity is a primary cue for attractiveness. On the other hand, masculinisation of the eyes, but not of the face outline, changes the perceived age of the target face.

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◆ **Eye-movement patterns reflect perceptual biases apparent in chimeric face processing**

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Studies of patients with focal brain lesions and neuroimaging indicate that face processing is predominantly based on right-hemisphere function. In addition, experiments with chimeric faces, where the left and the right sides of the face are different, have shown that observers tend to bias their responses toward the information on the left. Here, we monitored eye movements during a gender-identification task using blended face images for both whole and chimeric (half female, half male) faces (Burt and Perrett, 1997 *Neuropsychologia* **35** 685–693). As expected, we found a left perceptual bias: subjects based their gender decision significantly more frequently on the left side of the chimeric faces. Analysis of the first saccade showed a significantly greater number of left fixations independent of perceptual bias, presumably reflecting the tendency to first inspect the side of the face better suited to face analysis (left side of face/right hemisphere). On top of this, though, there was a relationship between response and fixation pattern. On trials where participants showed a left perceptual bias, they produced significantly more and longer fixations on the left. However, for trials where participants showed a right perceptual bias, there was no reliable difference between the number or length of fixations on the left or the right. These results demonstrate that on a trial-by-trial basis subtle differences in the extent of left or right side scanning relate to the perceptual response of the participant, although an initial fixation bias occurs irrespective of response bias.

◆ **High-level effects in rapid ‘pop-out’ visual search**

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Last year (2002 *Perception* **31** Supplement, 20) we showed that photographs of human faces pop out from a background of varied photograph distractors. This finding is in line with the reverse-hierarchy theory of vision (2002 *Neuron* **36** 791), which distinguishes between ‘vision at a glance’, a high-level and rapid, spread-attention, and generalising mode that detects points of interest and guides later ‘vision with scrutiny’, a slower process focusing attention on low levels, providing details to explicit perception. Here, we investigated when and how the ‘vision at a glance’ mode is activated. We show that the pop-out effect for human faces does not generalise to animal faces. Search for animal faces (also among varied photograph distractors) generated longer search times and search slopes were both larger and more widely distributed than search for human faces.

This finding suggests that the pop-out effect is specific for highly salient categories such as human faces. A second experiment was designed to investigate what elements of the face mediate the pop-out effect. Results of a search task with scrambled human faces indicated that search is mediated by the configuration of the face as a whole, rather than by detection of specific facial features. The finding that pop-out depends on holistic perception confirms the claim of the reverse-hierarchy theory that pop-out is a high-level effect.

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◆ **Evolving facial expressions by reverse correlation with 2-D noise**

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To study the ability of humans to read subtle changes in facial expression, we describe a novel application of the spatial reverse-correlation technique, consisting of adding samples of spatial noise to the image and categorising the results according to their effect on human perception of emotion. This added-noise method differs from the ‘bubbles’ technique of Gosselin and Schyns (2001 *Vision Research* **41** 2261–2271) in permitting an evolutionary development to novel forms. An ambiguous facial expression (Leonardo’s *Mona Lisa*) was taken as a base image, and different 50%-contrast binary noise samples were added on each trial. Twelve naïve observers judged the facial expression on each of one hundred trials and responded on a four-category scale from “very sad” to “very happy”. The noise samples were then summed according to the response category, the sum added to the face, and the process iterated. Thus, the expression could be rapidly evolved to conform to the observer’s implicit expression template. The expression seemed meaningful to the observers for each added-noise sample. The selected noise instances converged rapidly to a stable change of expression, making iterative noise cumulation an efficient method of evolving changes to explore the observers’ expression space (given the very low likelihood of jumping to the final expression in one step). Selection of subregions of the cumulated noise revealed that the smile was carried entirely by the shape of the mouth region; the perception of smiling in the eyes was solely attributable to a configurational effect projecting from the mouth region. We conclude that behavioural reverse correlation with 2-D binary noise is an efficient means of exploring a complex pattern space such as that of facial expressions, and even of ‘painting’ novel visual imagery.

[Supported by NEI 13025.]

OBJECTHOOD 2

◆ **Disappearance patterns of coloured gratings and illusory contours in motion-induced blindness**

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When a global moving pattern is superimposed on high-contrast stationary stimuli, the latter occasionally disappear for periods of several seconds [motion-induced blindness (MIB)]. When two adjacent collinear Gabor patches are presented, they disappear and reappear simultaneously, but when two orthogonal Gabor patches are presented, their disappearances are independent (Bonneh et al, 2001 *Nature* **411** 798–801). In this study, the pattern of disappearance for coloured gratings and illusory contours in MIB setup was investigated. In the first experiment, two collinear or orthogonal grating patches with the same or different colours were presented to the observers and they were asked to report the duration of simultaneous and sequential disappearance of the grating patches. The duration of simultaneous disappearance was significantly higher than that of sequential disappearance when both attributes (colour and orientation) were the same and significantly less when at least one attribute was different. In the second experiment, two illusory contours were presented in an MIB setup. The stimuli were two patches that contained an oriented illusory line induced by two line gratings abutting each other with a phase shift. The orientations of real grating lines and illusory lines of the two stimuli were either same or different. The duration of simultaneous disappearance was significantly higher than sequential disappearance when both attributes (real line orientation and illusory line orientation) were the same, and significantly less when real line orientation or both attributes were different. These results show that similarity of attributes other than orientation leads the stimuli to disappear simultaneously in the MIB setup.

[The author wishes to thank Reza Rajimehr and Amin Zandvakili for their helpful comments.]

◆ **Fusion or rivalry are contingent on the perceptual meaning of visual stimuli**

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When identical stimuli project to corresponding areas in the two eyes, a single coherent sensation is experienced. That this process of 'cyclopean vision' is not simply the result of 'fusing' information from the two eyes is evident in the phenomenon of perceptual rivalry. Thus, when different stimuli project to the same retinal location, the ensuing perception alternates in space and time between the two monocular views. Though fundamental for understanding vision, rivalry remains enigmatic, primarily because there is uncertainty about what competes for attention. Here, taking advantage of the fundamental phenomenon of colour contrast, we show that physically different monocular stimuli will fuse, not rival, when the stimuli are likely to have arisen from the same object at the same location in space. Conversely, when identical monocular stimuli are likely to represent different objects at the same location in space, rivalry is experienced. The data suggest that what competes for visual awareness is not the physical similarity between monocular stimuli, but the similarity in their perceptual meanings.

[Supported by EPSRC.]

◆ **Differential effects of grouping in the detection of parts in visual patterns by humans and monkeys**

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We carried out five experiments assessing the sensitivity of human and non-human primates to basic form of spatial organisation, by using simultaneous matching-to-sample (MTS) versions of embedded figure tasks. In experiment 1, six tufted capuchin monkeys (*Cebus apella*) received a visual pattern as the sample and had to identify the comparison stimulus featuring some of its parts. Accuracy was higher when the parts were ungrouped elements than when they formed structures of spatially interrelated parts. This was true irrespective of whether the sample stimuli were organised as closed (eg squares or circles) or open (eg crosses) shapes. In experiment 2, the sample featured the parts, and the comparison stimuli the whole patterns. Here the advantage for ungrouped elements disappeared. The results of the first two experiments were replicated in a third experiment featuring novel stimuli and the counterbalancing of task presentation across subjects. In experiments 4 and 5, one hundred and twenty-eight human participants were presented (in counterbalanced order) with the same MTS versions of embedded figure tasks and the same stimuli as those used with monkeys. In contrast with monkeys, the accuracy of human participants was higher for grouped parts. An advantage for closed shapes also emerged in humans. These findings suggest that human and non-human primates use different processes to segment a visual pattern into its component parts or to integrate these component parts into a whole figure.

◆ **Attentional modulations of perceptual grouping in the visual cortex**

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It has been proposed that perceptual grouping occurs early in vision. However, it is still in debate whether grouping is influenced by high-level cognitive functions such as attention. In the present study we recorded high-density event-related potentials (ERPs) to investigate neural mechanisms underlying the effects of task relevance and size of attentional spotlight on perceptual grouping in the visual cortex. Stimulus arrays consisted of local elements that were either evenly spaced or formed into separate groups; and subjects performed three different attention experiments: (i) discriminate orientations of perceptual groups; (ii) discriminate colours of dots around stimulus arrays; (iii) discriminate colours of fixation cross. Task relevance and enlarged attentional window enhanced sensory activities as early as 80 ms after stimulus onset with generators in the lateral extrastriate and medial striate cortex, respectively. Perceptual-grouping-related activities, which occurred between 80 and 120 ms and were localised in the calcarine sulcus, were weakened when stimulus arrays were of low task relevance and eliminated when stimulus arrays fell outside the attentional spotlight. The results provide electrophysiological evidence for attentional modulations of sensory and perceptual processing in the visual cortex.

◆ **A simple, feedforward mechanism for processing junctions**

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Neurons in the early visual system are often considered ‘edge detectors’. However, there is some psychophysical evidence that supports an alternative view, in which the junctions of edges are often more salient than edges themselves. We previously showed (Martinez-Conde and Macknik, 2001, SFN Annual Meeting, San Diego, CA) that single units in the LGN and area V1 of the awake monkey respond more strongly to junctions than to edges. These results suggested that junction processing may not be a subsequent stage to edge processing, but that junctions may in fact be a more optimal stimulus than edges for early, centre–surround receptive fields. Here we convolved simple, linear computational models of receptive fields in the retina/LGN and area V1 with visual scenes (both illusory and non-illusory) containing edges and junctions. The computational models predicted a subspace of angles and contrasts in which junctions are stronger stimuli than any possible edge. These results match our previous electrophysiological data from the awake monkey, and our qualitative perception of visual illusions in which junctions are more salient than edges. Moreover, the data are compatible with the idea of junctions being processed very early in the visual system (ie starting in the retina, with antagonistic centre–surround receptive fields), without the implication of high-level mechanisms, such as feedback loops or intracortical circuits.

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TUESDAY

POSTERS

ACTION, SELF-MOTION, OPTIC FLOW, AND SPACE PERCEPTION

◆ Grasping partly occluded objects

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In the last decade, Milner and Goodale [1995 *The Visual Brain in Action* (Oxford: Oxford University Press)] proposed that visual information used for object-directed action is processed by the dorsal visual system, whereas visual information used for perception is processed by the ventral visual system. Several studies suggest that dorsal representations are largely based on the veridical properties of the stimuli that are likely to be specified on the retina. However, in objects that are partly occluded, the veridical features of the stimuli are not always represented on the retina. We investigated whether maximum grip aperture (MGA), a measure of visuomotor performance, is scaled according to the veridical size of partly occluded targets. Participants grasped either an unoccluded square or an identical square with one corner occluded by black Perspex. A kinematic analysis revealed a significant difference in the MGAs from these two conditions. Another set of stimuli occluded by clear Perspex was used to test the possibility that these results were due to differences in haptic feedback introduced by the occluding element. No significant differences were found between the MGAs obtained with targets occluded by black or clear Perspex, suggesting that the difference between the occluded and unoccluded conditions was due to differences in haptic feedback. Taken together, these results suggest that the representations used to guide action towards partly occluded targets do represent the location of an occluded point in space, and that they are not limited to retinal information. Whether these representations are computed in the dorsal or ventral visual stream is a question for further research.

◆ The role of visual information about a target object and moving limb in the early stage of prehension

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We investigated how visual information about a target object and the subject's moving limb affect the control of grasping during prehension, especially in the early stage of movement. Eight participants were required to reach for and grasp a cylinder (diameter = 4 or 6 cm). Two liquid-crystal shutter plates, which were placed in the same horizontal plane (25 cm above the experimental table), were used to manipulate the visibility of the participant's moving limb and of the target. The plate nearer to the participant altered the view of the hand/limb, and the farther one controlled the view of the object. The conditions were as follows: (i) both plates were open during movement (normal condition); (ii) both plates were closed 0, 150, or 350 ms after beginning an arm movement (near-and-far condition); or (iii) only the near plate was closed 0, 150, or 350 ms after beginning an arm movement (near condition). A metronome was used to control the duration of movement (approximately 1100 ms). The results showed that shutting at 0 and 150 ms in the near-and-far condition caused a significantly larger finger aperture, while the timing of shutting in the near condition had little influence on the maximum finger aperture. Moreover, the mean time to peak velocity (TPV) was about 350 ms in every condition, so TPV is probably related to the availability of visual information for grasping control. These findings demonstrate that online visual information, especially that of the target object, is critical for grasping control in the early stage of prehension movements.

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◆ Multiple action representations of familiar objects with handles: An fMRI study

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Recent findings suggest that grasping a familiar object in an appropriate manner involves access to semantic knowledge. In this study, we explored the neural basis of this semantic involvement using event-related fMRI. Three types of object images were presented in a random order: familiar objects with handles (FH+), familiar objects without handles (FH-), and geometrical objects with a handle-like part (GH+). Subjects were then instructed to configure an appropriate hand shape for grasping the object. Common activations were found for all event types contrasted with the baseline condition (fixation only): right cerebellum, left occipito-temporal junction, left primary motor cortex, and left primary somatosensory cortex. Activations specific to each event were: (i) anterior part of rostral cingulate motor area for FH+; (ii) left anterior intraparietal

area (AIP) and right premotor cortex (PMv) for FH–; (iii) right intraparietal sulcus and bilateral middle temporal area for both FH– and GH+; and (iv) left frontal eye field and left precuneus for FH–. When contrasted with other experimental conditions, activations of subcortical areas were found for FH+. When grasping an object without any explicit graspable feature ('handle'), object affordance was extracted at AIP, and activated a specific motor schema at PMv. However, when the object to be grasped had a handle-like feature, this activated learned visuomotor associations at subcortical areas. Activation at the anterior cingulate showed that the switching among multiple action representations took place. These results imply that a 'direct' route from vision to action is essentially affected by semantic and associative factors.

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◆ **Anticipating translating versus transforming objects: Visual perception and grasping**

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Observers tend to misremember the stopping point of a movement or change as being further forward in the direction of movement or change, a phenomenon known as representational momentum. Recent findings suggest that this anticipation-like effect is stronger for changes in position (object translation) than for changes in shape or size (object transformation). Here, we asked subjects to judge the final distance between two spheres after this distance had been increasing or decreasing. The spheres were two separate translating objects or were connected to form a single transforming object (a dumbbell). Subjects performed a perceptual judgment task and a motor task in which they grasped the final objects. For grasping, the subject's thumb and index finger were attached to two robot arms (PHANTOM[®]) which provided haptic feedback and allowed us to measure the maximum grip aperture. Results from the perceptual task showed that subjects always remembered the final distance between the spheres as larger when that distance had been increasing compared with that when it had been decreasing, regardless of stimulus type. However, for the dumbbells, (a) the effect of transformation direction was reduced, and (b) there was a stronger bias to remember the final distance as smaller than it actually was. For grasping, only the dumbbells produced an anticipation-like effect (with subjects opening their fingers wider if the dumbbells were growing compared to when they were shrinking), even though the grasp locations were identical for both types of stimuli. Overall, while anticipation-like effects can be observed in both perception and grasping, these two effects were modulated in different ways by our stimulus manipulations and, when they did appear together, were uncorrelated for individual subjects.

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◆ **The consequences of head motor signals for the perception of 3-D surfaces: Head-banging for Helmholtz**

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We hypothesise that during the preparation of a head movement, the visual system predicts the likely resulting optic flow on the basis of the currently perceived 3-D layout and the intended trajectory in space. For example, when preparing to move to the right while fixating a point on a stationary surface, the visual system is primed to perceive a surface rotating to the left (with respect to the eye). We tested this hypothesis using a two-fold ambiguity in perceiving the tilt of a moving plane from optic flow (sometimes called 'tilt reversal'), in which first-order optic flow remains invariant under simultaneous reversal of tilt and angular velocity. Owing to this ambiguity, immobile observers perceive the two possible surface tilts with equal frequency, while observers that generate the same optic flow actively moving about a stationary virtual object show a bias towards the solution which is spatially more stationary (the one that rotates less in an allocentric reference frame—Wexler et al, 2001 *Vision Research* **41** 3021–3035). As predicted by our hypothesis, we have found that a similar but significantly smaller bias can be induced in observers moved passively. Conditions where only motor signals were informative with regard to the orientation of the surface, or where a mismatch between motor signals and visual simulation occurred, resulted in performances comparable to those under immobile conditions.

◆ **The detection of motion in any reference frame**

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It is important to be able to detect objects that move with respect to oneself as well as those that move in an Earth-fixed, allocentric reference frame. It is known that moving objects are detected more efficiently than stationary ones (Ivry and Cohen, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 1045–1057), but since experiments were conducted on immobile observers, it is not known whether it is egocentric or allocentric motion that is detected. We dissociated the two types of reference frame by working with observers that move the head and/or the eyes, and studying the detection of objects whose motion is yoked to that of the observer. Thus, we were able to create motion selectively in any given reference frame. We have found that motion that is solely allocentric (no retinal slip or motion with respect to the head) is detected as efficiently as motion on the retina.

◆ **Transformation of spatial short-term memory representation for body rotation**

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We used a pointing task to examine the transformation process of spatial memory representation after body rotation. We presented a red target point 2 m ahead of the subjects, either under an illuminated or under a dark condition. During a 3 s delay period, the subjects rotated their body including the head by 70° to the right or left, and pointed to the remembered target location. In both conditions, pointing errors deviated in the opposite direction to body rotation. In the dark condition, the magnitude of the error was a linear function of the target position relative to body location before rotation, and twice as large as when subjects were stable from target presentation to pointing (Yoshida and Inui, 2001 *Perception* **30** Supplement, 85). Pointing errors in the illuminated condition could be explained quantitatively by the weighted sum model of the error in the dark condition and the error that was assumed to be based only on the spatial representation encoded in the frame of the target presentation area. These findings suggests that (i) in pointing tasks after body rotation, body-centred and environment-centred spatial representations are utilised in an integrative way; the former is referenced to the body location before rotation and the latter is referenced to the selected object that is observable at body locations before and after rotation, and (ii) body rotation magnifies pointing errors derived solely from the body-centred representation in the direction of the pre-rotation body location approximately by a factor of two.

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◆ **Visuo-spatial memory in dancers: Selection of the reference frame**

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We investigated the spatial memory of visual target location and the effect of training. Seated on a motorised chair, nine control subjects and eight professional dancers, all right-handed, were presented with a straight-ahead visual target. The chair then rotated by 90°, 180°, or 270° around the vertical axis, rightward or leftward, in complete darkness. 10 s or 25 s after the rotation, subjects had to return to the previously seen target orientation, driving the chair with a joystick. In order to fulfil the task, the subjects could either reproduce the imposed rotation in the inverse direction (ego-centred inversion strategy), or continue the rotation up to 360° in the same direction (exo-centred completion strategy). The non-dancers chose the completion strategy in 14% of all trials, versus 28% for the dancers. The gain in inversion decreased with increasing stimulus angle, while that in completion increased. The gain in inversion was close to 1 with a variability (SD) of 20%, while that in completion had 60% variability. Response duration was longer with non-dancers (and longer than the stimuli), apparently because of hesitations. For both groups, the inversion gain of rightward stimuli was higher than that of leftward stimuli (ns), and was not affected by the delay. However, the completion gain was higher after the short delay than after the long delay with dancers (significant only for leftward stimuli). These preliminary results show that the location of a landmark is better encoded with the ego-centred reference frame, and that training increases self-confidence.

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◆ **A sensory – motor approach of colour perception**

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Why is it that we perceive a richly coloured world everywhere in our visual field, even though the colour signals provided by the peripheral retina are quite poor? In a sensory – motor approach, visual experience derives from acquired knowledge of the laws coupling sensory inputs with the observer's movements. In our experiment, subjects are asked to pursue a figure on a screen, while the whole screen colour (or luminance) changes according to the position of the figure. Even if, at every moment, the screen is homogenous, a strong gradation effect appears, suggesting that colour perception in periphery is strongly affected by prior knowledge acquired during visual exploration. We investigate whether this gradation effect is compatible with our sensory – motor theory, and in particular whether, after a long adaptation to the systematic colour/gaze-direction correlation, the effect disappears, as the theory would predict.

◆ **Sensory – motor approach to shape recognition**

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According to a radical sensory – motor approach, we postulate that action is a constituent of perception. Instead of considering the sensory input flow, our alternative approach to shape recognition proposes that we focus only on the motor commands involved during interactions with the object. The experiment uses a mobile robot, whose sensory inputs are linked to the motor commands so as to produce a sensory – motor coupling that forces the robot to exhibit a 'wall following' behaviour and makes it turn around the encountered objects. Through this behaviour, sensory flow and command sequences are strongly structured. Motor commands, far simpler than the sensory flow, allow the online learning of new shapes, thanks to a dynamic categorisation system, which also permits anticipation and faster recognition when the object is encountered again.

◆ **Mental extrapolation of target position is strongest with weak motion signals and motor responses**

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Some accounts hold that the position of moving objects is extrapolated either in visual perception or visual short-term memory ('representational momentum'). However, some studies did not find forward displacement of the final position when smooth motion was used, whereas reliable displacement was observed with implied motion. To resolve this conflict, the frequency of position changes was varied to sample motion types between the extreme cases of implied and smooth motion. A continuous function relating frequency of target change and displacement was found: displacement increased when the frequency of position changes was reduced. Further, the response mode was varied. Relative judgments produced less forward displacement than absolute judgments such as mouse or natural pointing movements. Also, localisation judgments were susceptible to context effects, but not to variations of probe stimulus or expectancy about the motion path. It is suggested that forward displacement results from the extrapolation of the next step in the observed motion sequence.

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◆ **Form – motion integration for perception and action**

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Visuo-manual coordination involves an adaptive interplay between sensory processing and motor control. It has been suggested that distinct anatomical pathways convey perceptual identification and on-line visuo-motor control. In this context, we studied whether form and motion binding is achieved differently in passive viewing condition and during active behaviour. In 'passive' condition, six subjects had to evaluate on a numerical scale the perceptual coherence of rigid outlined shapes (diamond, cross, and chevron) translating clockwise or counterclockwise along elliptic trajectories, behind static apertures of varying visibility. In two separate 'active' conditions, a graphic pen was used to drive the stimuli along cued trajectories and to track their perceived centre along uncued trajectories. Subjects were asked to evaluate the perceptual coherence of the stimuli at the end of each trial. No visual feedback of the active hand was given during the task. Results show that the visibility of apertures in combination with the type of shape strongly affect perceptual reports, both in the passive and active conditions. Motor performance is highly correlated with perceived coherence: in the driving condition, movement path is smoother at high compared to low coherence, suggesting that observers do not rely exclusively on proprioceptive

feedback; in the tracking condition, the phase lag relative to stimulus position increases as perceived coherence decreases. Altogether, the results suggest that active behaviour does not facilitate the spatiotemporal binding of component motions and are not compatible with the view that vision-for-perception and vision-for-action are processed independently through distinct cortical pathways.

◆ **Motor and visuospatial asymmetries: Which come first?**

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According to a classical explanation, asymmetries of motor habits determine the asymmetries of visual space. Evidence recently collected by Marino and Stucchi (2001 *Perception* 30 Supplement, 25) that the left–right asymmetry of visuospatial representation is driven by handedness seems to support this explanation. Nevertheless, since handedness is not directly manipulated, the critical account that the presence of asymmetries in visual space is not the results but the origin of motor asymmetries cannot be excluded. To test this possibility, we compared blind and blindfolded left-handers and right-handers, in tabletop line retracing task. Participants were required to draw on a digitiser tablet lines with free length and orientation. As they complete each line production they had to return to the starting position running the pen over the way previously covered. Asymmetries in the line production as well as in the line reproduction were found for both blind and blindfolded participants. The result that the performance in the line retracing task is asymmetric even for individuals who cannot visually represent external space indicates that motor asymmetries are prior to visuospatial asymmetries.

◆ **Action-related intentional effects in a visual search task**

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The aim of the current study was to test if visual features relevant to the task are processed more efficiently at an early, presumably parallel, level, compared to irrelevant target features. Subjects either had to grasp or point at a target. It was hypothesised that since orientation, in contrast to colour, is relevant to the action of grasping, enhancement of orientation-discrimination performance should be selective. The visual search task required searching for a conjunction of a particular colour and orientation. Subjects viewed stimuli on a screen while their gaze was tracked to determine the targeting of the first saccade. Target–distractor discriminability and set size were manipulated. In experiment 1, the difficulty of colour and orientation search was matched so that subjects would make 50% errors in feature search. In experiment 2, the colour contrast of target and distractors was decreased. There were two levels of set size of the search display. Enhanced orientation discrimination (relative to colour) was found for the condition in which subjects grasped the target compared to the condition in which they pointed towards the target. The action effect was most prominent in the small set-size, high-discriminability condition, and weakest in the large set-size, low-discriminability condition, with intermediate effects for the other two conditions. Action intention selectively enhances the processing of a behaviourally relevant feature. Signal detection modeling indicates that our results can be explained on the basis of an enhancement of an early and possibly parallel stage of feature processing.

◆ **Saccadic adaptation influences pointing localisation of transient stimuli**

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Visual localisation during saccadic eye-movements is severely distorted: a vertical bar briefly flashed just prior to a saccade is perceived close to the saccadic target. However, if subjects point blindly to the bars, they respond correctly (Burr et al, 2001 *Current Biology* 11 798–802). Another case of visual mis-localisation occurs under conditions of short-term saccadic adaptation, when the saccade target steps in a stereotypical way during the eye movement; after a few trials the eye moves straight to the final position of the target. Perceptual mis-localisation during conditions of saccadic adaptation takes place for targets presented peri-saccadically, but also for targets presented up to 400 ms before the saccade. Here, we study whether motor adaptation of eye movements can also alter localisation of objects by pointing. We measured localisation by blind pointing during fixation, normal saccade, and adapted saccade for bars presented for 4 ms well before a saccadic eye movement. Localisation performance for transient bars during fixation is linear, but not veridical, indicating an effect of gaze position on pointing. Executing a normal

saccade does not alter the mis-localisations observed during fixation for bars presented 150 ms before the saccadic onset. However, during adaptation, there is a significant shift of the pointing in the direction of adaptation, similar to the perceptual one observed in the previous studies. These results indicate that saccade adaptation induces a long-lasting distortion of the visual space that is transferred to other motor actions (like pointing) as well as to perceptual localisation.

◆ **Moving the eyes along the mental number line: comparing SNARC effects with saccadic and manual responses**

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Bimanual parity judgments about numerically small (large) digits are faster with the left (right) hand, even though parity is unrelated to numerical magnitude per se (the SNARC effect; Dehaene, 1992 *Cognition* **44** 1-42). According to one model, this effect reflects a space-related representation of numerical magnitudes ('mental number line') with a genuine left-to-right orientation. Alternatively, it may simply reflect an overlearned motor association between numbers and manual responses, as for example on typewriters or computer keyboards, in which case it should be weaker or absent with effectors whose horizontal response component is less systematically associated with individual numbers. Two experiments involving comparisons of saccadic and manual parity judgment tasks clearly support the first view; they also establish a vertical SNARC effect suggesting that our magnitude representation resembles a number map rather than a number line.

◆ **Fast reaction to a change in target size**

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The ability to respond quickly to new visual information is essential for such information to be useful for the online control of action. It is known that people need only about 100 ms to respond to a change in target position or orientation. It takes them much longer to respond to other characteristics. A reason for this may be that, in daily life, peoples' relationships with surrounding objects (positions, orientations) are constantly changing, while features of the objects themselves (colour, shape, size) normally do not change. In order to evaluate whether this could be the reason for the different latencies, we examined how quickly subjects could respond to a change in size. We used a pointing task, for which we know that people are able to respond quickly to a change in position. Subjects moved a stylus across a digitising tablet from a specified starting point to two targets in succession. The first of these targets was always at the same position but it could have one of two sizes. The second was always at the same place and of the same size. Not surprisingly, subjects moved faster towards the first target when it was larger. On some trials the target changed size at the moment the subject started to move. When the target started by being big, but changed to being small as soon as the subject started moving, the peak velocity decreased significantly. Since peak velocity was reached only about 150 ms after the change in size occurred, this means that subjects can react very quickly to changes in size. We conclude that the proposed distinction is not the reason for differences in response latency.

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◆ **Demonstrating unconscious cognition: Three types of dissociation**

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Direct measures (*D*) for visual perception try to assess visual awareness for a critical stimulus, whereas indirect measures (*I*) are used to indicate whether the stimulus was processed at all. Problematically, both measures might be influenced by conscious as well as unconscious stimulus information (Reingold and Merikle, 1988 *Perception & Psychophysics* **44** 563-575). We analyse dissociations between *D* and *I* as indicating unconscious processing by converting them to an effect-size scale and plotting them against each other. (i) The empirical finding of a nonmonotonic relationship between *D* and *I* suffices to demonstrate unconscious processing under minimal measurement assumptions, even if the critical stimuli are visible. (ii) Null sensitivity in the direct measure ($D = 0$, $I > 0$), the traditional criterion for unawareness, is sufficient for demonstrating unconscious processing only under strong additional assumptions. (iii) If *D* is at least as valid a measure for visual awareness as is *I*, the finding that the indirect effect exceeds the direct one ($I > D$) is sufficient but requires comparable scales of measurement. We present

experimental data from an action-priming paradigm (Vorberg et al, 2003 *Proceedings of the National Academy of Sciences of the USA* **100** 6275–6280) demonstrating all three types of dissociations.

◆ **Sub-criterion stimuli do not affect the motor system**

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Numerous experiments seem to indicate that visual stimulation can influence the motor system without mediation by its conscious perception. A cornerstone of the divorce of the perception–action couple is the alleged finding in metacontrast experiments that masking may prevent the perception of visual information, but not the activation of motor processes. However, most studies did not assess the observers' perceptual performance by measuring both the visibility of the masked stimulus (d') and the observers' response criterion (c), as proposed by the signal detection theory. This prevents an answer to the question whether the trigger of a motor response depends on the perceptual internal response exceeding a (perceptual) criterion or on some unrelated threshold proper to the motor system. We present a metacontrast paradigm allowing the measurement of both the observers' perceptual and motor behaviour elicited by the same, close to threshold, stimulus on a 'trial-by-trial' basis. On any given trial, the reaction time (RT) to the occurrence of any of two (masked and masking) stimuli was recorded together with the observers' subsequent response on the presence/absence of the masked stimulus. We analysed RTs as a function of both the presence/absence of the masked stimulus and the observers' internal state (stimulus reported or not). In addition, the manipulation of the strength of the masked stimulus (ie contrast; hence d') and of its probability of occurrence (hence the response criterion, c) permitted the assessment of the impact of the visibility proper of the stimulus and of the observers' response criterion (decisional behaviour) on the RT. Preliminary data show that masked stimuli affect RTs only if they are consciously perceived, ie if their internal responses exceed the perceptual criterion. This result is contrary to what would be expected if perceptual and motor processes were independent.

◆ **Role of stereoscopic information in self-motion perception from expanding/contracting optic flow**

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Expanding and contracting flows were presented with binocular disparity to investigate the role of stereo depth in vection. In experiment 1, we presented expanding and contracting flows simultaneously on different disparity planes. Subjects reported whether they felt forward or backward self-motion. The results showed the dominance of the stereoscopically farther flow in determining self-motion direction. In experiment 2, two expanding flows were presented on different disparity planes. The centre of each expansion was displaced horizontally to either side. Subjects judged in which direction they were going when they felt forward vection. The results showed that the subjects felt their heading biased to the direction of the centre of the farther expansion. The heading was determined solely by the farther flow, not by 2-D integration of retinal motion. We also observed a reversed-disparity expanding/contracting flow that originally simulated a tunnel. That is, the centre (peripheral) region of the flow was stereoscopically near (far). Elements in the expanding (contracting) flow seemed to get farther (closer) as the flow expanded (contracted). Although vection strength was reduced under this condition, expanding (contracting) flow still induced forward (backward) vection. These results demonstrate that stereo depth is important in determining the flow to be analysed. But disparity information itself may not greatly contribute to analysing an optic flow.

◆ **Neural correlates of categorical and metric spatial relations: An event-related fMRI investigation**

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Event-related functional magnetic resonance imaging (ER-fMRI) was applied to investigate brain activation involved in the representations of spatial visual relations. Two spatial visual relation tasks were used to test the hemispheric specialisation hypothesis in the processing of metric (that specify the distance between two objects) and categorical (that specify the object position relative to another one) spatial relations. The metric judgment task required the participants to estimate whether a dot was within or beyond a criterion distance with respect to a horizontal

bar, while the categorical judgment task required the participants to estimate whether the dot was above or below the bar. In a block-design fMRI experiment, Baciú et al (1999 *NeuroReport* **10** 1373–1378) had previously shown a right angular gyrus advantage in the metric task and a left angular gyrus advantage in the categorical task. Moreover, a practice effect had been observed in the metric task, which was revealed by a decrease with time of the activation within the right angular gyrus. Using an ER-fMRI paradigm allowed us to isolate activation relative to each stimulus and to address the question of activation specificity depending on the position of the dots relative to the criterion distance (far from it or close to it). Results revealed, in the metric task, a right angular gyrus activation for both conditions. In the categorical task, they showed left putamen activation. In addition, right angular gyrus activation observed in the first part of the metric task disappeared in the second part of the task. Results are interpreted in terms of new categorical representations emerging during the practice of the metric task.

◆ **Effect of observer's self-motion sensation on scene recognition in immersive virtual-reality environment**

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In this study, the recognition of objects' layout across views was examined in the immersive virtual-reality (VR) environment called CABIN. It has five screens (2.5 m each) which are arranged like a cube surrounding an observer. An observer views the image dichoptically through LCD shutter glasses. Thus, the observers can immerse into 3-D VR environment. Using one screen 2-D VR environment, we have reported that the performance of scene recognition depended on visually induced self-motion sensation [Kitazaki and Yoshino, 2002 *Journal of Vision* **2**(7) 633a]. The purpose of the study was to examine whether our scene representation is renewed by the visual information of the self-motion in the immersive 3-D VR. We constructed a virtual room in CABIN and set a table at the centre of the room, on which five geometrical objects were randomly located. A trial consisted of a memorisation phase (3 s), a retention phase (7 s), and a recognition phase (3 s). In the retention phase, the table and/or the room were rotated 47°, while the objects on the table were occluded and one of them moved to a new position. Room rotation simulated viewpoint movement. The observers were required to identify the moved object. When recognition was made from same viewpoint (without room rotation), the performance was more accurate in the condition of the same retinal image of the layout of the object (without table rotation) than of a different retinal image. However, when recognition was made from a different viewpoint (with room rotation), the performance was more accurate with the different retinal image, which was consistent with viewpoint movement in the real-world. These results suggest that our scene representation can be renewed automatically and inevitably by visual self-motion simulation in the immersive 3-D VR.

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◆ **The role of eye height in the detection of affordance through base-up prisms**

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We investigated the role of eye height in the detection of affordance [Gibson, 1979 *The Ecological Approach to Visual Perception* (Boston, MA: Houghton Mifflin); Warren, 1984 *Journal of Experimental Psychology: Human Perception and Performance* **10** 683–703]. In a base-up prisms condition and in a baseline condition, participants made judgments of their maximum seat height ($S_{h\max}$) and other participants made judgments of the minimum height of a horizontal barrier under which they could pass ($B_{h\min}$). The perceived eye height was measured (see Mark, 1987 *Journal of Experimental Psychology: Human Perception and Performance* **13** 361–370; Wraga, 1999 *Perception & Psychophysics* **61** 490–507). These judgments were made in two visual conditions, in a 'natural' visual context and in a dark surrounding. The results showed that, whatever the visual conditions, base-up prisms lead to an overestimation of the perceived eye height and $S_{h\max}$ and in an underestimation of $B_{h\min}$. Furthermore, a clear effect of adaptation was found. In experiment 2 we made a comparison with haptic judgments. Our results confirm the role of eye height in the perception of maximum seat height and provide direct support for the role of eye height in the estimation of minimum aperture height. These results show that the eye level is calibrated in relation to the visual optic array and serves, in return, for the estimation of the relative height of surfaces for certain actions of the organism.

◆ **Effects of shape and noise on speed perception—its implications for road design**

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Our previous study has demonstrated that shapes of surface patterns on the road influence the speed of motion perceived by observers even when the test pattern moves with the same speed. It has also been found that the relationship between the orientation of pattern components and the direction of motion is critical in determining the perceived speed. However, the motion of the test pattern used in that study was restricted only to the upward–downward direction, and therefore the results could not be applied to the road environment design, because in real driving conditions we perceive rather motion in depth or radial motion. In the present study, we examined how the perceived speed in the road environment was affected by changing the shape of the road surface and the noise level. As test animations of road scenes, four different configurations of traffic lane were used: straight centre lane, straight right lane, curved centre lane, and curved right lane. For each road scene, the physical speed was varied in six steps and the noise level was varied in three steps. Therefore, each of four test animations included 18 speed–noise combinations which were presented randomly. Participants were asked to judge the perceived speed of each test animation using the method of comparative magnitude estimation. The results indicated that the lane shape and noise level influenced the perceived speed. It was also found that louder noise facilitated the overestimation of speed. The speed on the curved lane tended to appear faster than on the straight lane; the speed on the curved right lane was overestimated by the presence of the elements of road surface and background such as painted stripes or trees. Implications of these findings for road design are discussed.

◆ **Perceived distance of travel estimated from accelerative and decelerative optic flows along straight and curved lines**

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Physical length can be derived from acceleration and initial velocity in an accelerated motion by using a double-integral computation. However, it is not known how the human visual system perceives acceleration and deceleration, or estimates distance of travel with an accelerated optic flow. To clarify characteristics of acceleration perception induced by optic flow, we conducted two experiments in which subjects estimated perceptual distance of travel in a heading motion derived by observing an optic-flow stimulus which simulated locomotion in a virtual tunnel (W 1.7 m, H 1.7 m) with a constant acceleration or deceleration with an initial velocity (ranging from 0 to 8.4 m s⁻¹). The stimulus (W 106 deg, H 90 deg) was presented on a screen (W 2.2 m, H 1.7 m) by an LC projector. The moving paths were straight (experiment 1) and curved (experiment 2) with three radii of curvature (3.3, 6.6, and 13.2 m). Subjects were not informed that the accelerations were constant. The results of experiment 1 showed that subjects can estimate the perceptual length reliably despite the sign of the acceleration but the accuracy depends on the subject. On analysing the results by using physical formulation, it is found that perceptual accelerations tend to decrease with increasing simulated acceleration and duration. The results of experiment 2 showed that a curved path induces longer perceptual migration length than the straight path, suggesting that perceptual acceleration and perceptual distance of travel depend on the velocity distribution of optic flow.

◆ **Visuo – vestibular interaction(s) in the reconstruction of passively travelled manoeuvres**

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We recently published a study of the reconstruction of passively travelled manoeuvres from optic flow (Bertin et al, 2000 *Vision Research* 40 2951–2971). Perception was prone to illusions in a number of conditions, and not always veridical in the others. Part of the illusory reconstructed manoeuvres could be explained by assuming that subjects base their reconstruction on the self-motion percept built during the initial moments of the stimulus. We tested this hypothesis using a novel paradigm: if the final reconstruction is governed by the initial percept, providing additional, extra-retinal information that modifies the initial percept should predictably alter the final reconstruction. The extra-retinal stimulus was tuned to supplement the information that was under-represented or ambiguous in the optic flow: the subjects were physically displaced

linearly or rotated in place at the onset of the visual stimulus. A highly asymmetric velocity profile (high acceleration, very low deceleration) was used. Subjects were required to guide an input device (in the form of a model vehicle; we measured position and orientation) along the perceived manoeuvres. We confirm that a short-lasting vestibular stimulus can influence the perception of a much-longer-lasting visual stimulus. Perception of the self-motion translation component in the visual stimulus was improved by a linear physical displacement: perception of the self-motion rotation component by a physical rotation. This led to a more veridical reconstruction in some conditions, but to a less veridical reconstruction in other conditions.

◆ **Optic-flow-based estimation of travel distance in virtual environment**

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Because optic-flow speeds induced by self-motion depend on the dimensions of the environment, distance estimation from optic flow is possible only when speeds can be calibrated from other sources of depth information, such as binocular disparity or known geometrical properties of the environment. For instance, in a ground-plane environment with fixed eye height, discrimination of the distances of simulated self-motions of different speed and duration is reliably possible from optic flow. Following up on this study, we ask whether a distance estimate obtained from optic flow in a realistic ground-plane environment can be transformed into a spatial interval in the same visual environment. Experiments were conducted in a computer-animated virtual environment (CAVE) with completely immersive, stereographic, head-yoked projection, that extended 180° horizontally and included the floor space in front of the observer. Observers viewed a stimulus depicting self-motion over a random-dot ground plane with variable speed and duration. Simulated distances ranged from 2.2 m to 13 m. Afterwards, the screen depicted a stationary view of the scene and two horizontal lines appeared on the ground in front of the observer. Using a pointing device (CubicMouse), the subject had to adjust the interval between these lines to match the distance travelled during the movement simulation. Interval size increased linearly with simulated travel distance. Hence observers could obtain a coherent distance measure from optic flow. However, subjects consistently underestimated distance by 33% (slope of regression 0.67). We conclude that optic flow can be used to derive an estimate of travel distance, but this estimate is subject to scaling when compared to static intervals in the environment.

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◆ **Perceived spatial layout in static and motion displays seen at different slants**

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Photography, images, and virtual scenes seen at a slant show distorted optical projections compared to their corresponding real counterparts. Previous studies yielded contradictory data about the effect of viewpoint displacement (VD) on size, form, or slant perception of objects. However, most studies of the ability of subjects to compensate for geometrical distortions used static displays. Our purpose was to investigate VD effect in a virtual scene depicting either a static subject viewpoint or his/her simulated displacement in the virtual scene. Moreover, we had to establish if beyond 45° the deformation in moving images was effectively disturbing. Participants were required to estimate the location of several objects in a virtual scene (as viewed by a static or a displacing observer) presented on a slanted screen. Viewing angles were 0°, 35°, and 70°, and chosen below and above the previous threshold of 45° measured by Meister for distortion in motion pictures. We recorded both depth and lateral estimations. Results indicate differences between static and motion conditions only for some configurations of objects and a variable effect of viewing angle according to depth and lateral estimations. Human ability to compensate for distortions is highly dependent on the type of spatial layout in static and motion displays. The effect of viewing angle is present for both kinds of display, but only with an extreme slant, and affects mainly lateral estimations.

◆ **Perceived slant defined by two types of motion**

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Surface slant can be defined by two types of motion: a radial motion and a translational motion. Forward or backward motion of observers parallel to a surface slanted around a horizontal axis produces radial motion, while their lateral motion parallel to the surface produces translational

motion. It is suggested in the literature that parallax depth system is more sensitive to shear transformations—analogue to translational motion—than to expansion/contraction transformations—analogue to radial motion (Rogers and Graham, 1983 *Science* **221** 1409–1411). In the present study, we compared slant perception defined by the two types of motion in terms of the threshold and perceived extent. Random-dot motion was produced with OpenGL and presented on a 21-inch CRT display; dot speed at the centre of the display was either 1.4, 2.7, or 5.5 deg s⁻¹. Stationary observers viewed the stimulus, at a distance of 57 cm, through a tube confining the visual field to 10 deg. Each of approximately 190 stimulus dots had a lifetime, so that the dot density could not be a cue for the surface slant. Threshold of slant perception in terms of dot lifetime was lower for radial motion than for translational motion, while perceived extent of slant was equal for the two types of motion. The results are not consistent with the suggestion provided by parallax depth perception experiment, maybe because of the difference of observers' perception and task (eg stationary or moving). The results suggest the following: (a) the visual system is more sensitive to speed gradients along the direction of motion than those in the direction orthogonal to the motion, and (b) the visual system corrects the sensitivity difference between the two types of motion at suprathreshold level.

◆ **Perceived direction and distance of self-motion from visual and vestibular sensory integration**
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We examined whether intermodality integration between visual and vestibular systems follows vector summation. In experiment 1, we measured the perceived direction of self-motion from synchronised visual and vestibular motion information, and which directions were orthogonal. Expanding/contracting random-dot patterns were used to produce forward/backwardvection. A swing was used to provide rightward/leftward motion stimulation to vestibular system with continuous acceleration. Subjects fixed their heads on a chin-rest that was mounted on the swing, and observed motion stimuli through a head-mounted display. They performed a rod-pointing task to report the perceived direction of self-motion. Results showed that a mid-way direction between visual and vestibular information was perceived. In experiment 2, we measured the perceived direction when the expansion/contraction rate was varied. Subjects reported the perceived distance by magnitude estimation, in addition to the perceived direction from the rod-pointing task. Results showed that the perceived direction was constantly at the mid-way, though the low, middle, and high rate of expansion/contraction produced short, middle, and long perceived distance, respectively. These results suggest that the direction of self-motion is processed independently, ie the intermodality integration between visual and vestibular systems does not follow vector summation.

◆ **Effects of visual field on perceived speed of self-motion from optic flow**
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Optic flow fields provide information for heading speed. We investigated the effects of retinal area and retinal position of radial flow on perceived self-speed. To do this, we conducted two experiments in which observers viewed a radial flow, while fixating a point at a focus of expansion of the flow-simulating translation through a cylindrical tunnel whose inner surface was filled with random dots. The diameter of the tunnel was 4 m, while the simulated heading speed was either 18 or 72 km h⁻¹. In the first experiment, we investigated the effect of stimulus area. For the test stimulus, flow field was curtailed radially, and its area was either 5%, 12%, 25%, and 50% of the whole screen. The staircase method with temporal alternative forced-choice algorithm was used to determine the perceived self-speed with the test stimulus compared to that with the flow on a whole screen. The results showed that the perceived self-speed increased gradually with stimulus area. In the second experiment, we investigated interaction between stimulus area and retinal position. For the test stimulus, flow field was curtailed so that the stimulus was presented within or outside a circular border. The diameter of the circular border varied between 20, 40, or 60 deg. The results showed that the perceived self-speed increased with the border size for both the stimulus presented within and outside the border. These results suggest that the perceived self-speed has large integration fields, extending over 60 deg, and is affected by perceptual error of three-dimensional information.

◆ **Egocentric visuomotor adaptation**

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Previous research has shown that humans generalise perturbations of visuomotor feedback in terms of egocentric rotations. We investigated whether this adaptation involves changes in visual localisation (relative to the eyes) or changes in proprioceptive localisation (relative to the shoulder). We asked subjects to align an unseen cube with a 5 cm side with a simulation that they saw via a mirror. Subjects made successive movements between target locations in a sequence of adaptation and test phases. During adaptation phases, subjects received either veridical or perturbed visual feedback about the real cube. The perturbations were consistent with a change in azimuth either relative to the eyes or relative to the shoulder. During test phases, subjects received no visual feedback. We compared test movement endpoints after perturbed feedback with ones after veridical feedback. Despite the similarity between the perturbations, the spatial layout of the shifts in endpoints clearly reflected the small differences between the two perturbations. In a second experiment we investigated intermanual transfer of adaptation to determine whether the shifts in endpoints were due to changes in visually perceived location or to changes in the proprioceptively perceived location of the hand. Changes in visual localisation are not specific to either arm and should transfer to the arm that was not exposed to the perturbed feedback. We found that the transfer of adaptation to the unexposed arm was substantial but incomplete for both types of perturbations, indicating that the adaptation to both types of perturbations was not specifically linked to either visual or proprioceptive localisation.

◆ **Perceptual velocity thresholds for a moving ground texture**

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The aim of this research was to study the perception of the velocity of optic flow. The flow was projected onto a large floor (5 m × 10 m) on which the participants stood upright. In this kind of situation they must in fact estimate an optical velocity gradient. The texture flow generator (TFG), used to project a moving texture of circular luminous dots onto the ground, was the same as the one used to record produced speed in locomotor performances in previous experiments. In three experiments with different psychophysical methods, subjects had to reproduce, with a joystick, the visual speed presented in different gaze position. The differential thresholds ranged between 10% and 20% and increased with global optical velocity. No significant effect is observed from the different gaze positions. These thresholds are much higher than those observed in an adjustment of the speed of locomotion in the same optical environment. The results demonstrate that the estimation of the velocity of a texture when standing still (as in the present experiments) involves different perceptual processing from that when perception is coupled with a displacement of the participants, as in walking. Moreover, the data also hint at the difficulty of extrapolating from classical psychophysical results, obtained with stimuli on small vertical screens and homogeneous textures, to the perception of optic flow in a large visual environment.

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◆ **The effect of scenery richness and motion parallax in simulator sickness**

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Our aim was to determine to what extent the retinal flow resulting from scenery richness and the gaze axis are involved in 'simulator sickness' during driving-simulation tasks. Manipulations of retinal flow components were linked to visual display characteristics (rich or poor in terms of the quantity of elements present in the display). Gaze axis was manipulated by changing the ratio between real and simulated axis (motion parallax distortions), with a truck-driving simulator, in which subjects had to drive under four scenery and gaze manipulation conditions. Motion sickness was measured during each trial (every minute) on a Lickert scale (0 = 'I feel good', 10 = 'vomiting'). The subjects' sensitivity to sickness was evaluated on a Graybiel scale before and after each session. Results show that subjects had the tendency to be more sick in a rich visual environment. This effect was particularly strong when the real gaze axes deviated extremely from the simulated ones (corresponding to the highest level of motion parallax distortion). Considering that perception is also an anticipation of action consequences, our results suggest that motion sickness is linked to the so-called 'expectation violation' approach.

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◆ **Locomotion and static-scene analysis: Attentional and encoding constraints**

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Gibson [1950 *The Perception of the Visual World* (Boston, MA: Houghton Mifflin)] proposed that a fundamental source of information for locomotion is optic flow. We have recently been examining an additional source of information based on an analysis of static scenes that includes angular direction and layout. According to this analysis, observers recover coarse spatial information regarding layout that is encoded and available for long durations. In addition, this analysis uses landmarks within the scene and requires attention. To examine this analysis our experiments present observers with two digitised images of real-world scenes or computer-generated scenes in which the camera position/viewpoint has changed consistent observer movement in the scene. The ISI between frames is sufficiently long in some conditions (1000 ms) to prevent the appearance of apparent motion and thus the availability of optic flow information. The observer's task is to indicate the direction of motion after viewing the two frames. Experiments are presented that examine (i) the role of attentional load manipulated by performing a concurrent secondary task; (ii) the importance of ordinal information of landmark layout; and (iii) the role of position information of landmarks. The results of these experiments indicate that attentional load is only a factor when ISIs are sufficiently long to prevent apparent motion. In addition, changes in the ordinal layout of landmarks reduces accuracy in the judgments of direction of motion at long ISIs. However, performance during altered ordinal layout conditions was above chance, suggesting that observers are also encoding position information of landmarks independently of landmark identity. The encoding limitations of recovering layout information from landmarks under these conditions are also discussed.

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◆ **Steering control from optic flow of radial and lateral motions**

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Human observers extract self-motion information from optic flow to perceive heading direction and to control steering and posture. When a lateral motion is superimposed on an expanding radial motion, the focus of expansion and heading perception are illusory biased in the direction of the lateral motion (eg Royden and Hildreth, 1996 *Perception & Psychophysics* **58** 836–856). This is inconsistent with the prediction based on velocity summation of two motions. In contrast, we have reported that the visual control of posture from the same stimulus utilised the velocity summation (Kitazaki and Kurose, 2003 *VSS03 Proceedings* 155). The purpose of this study was to see if the visual control of steering is influenced by the illusory heading perception or velocity summation. Subjects were asked to control steering to make the car go straight through a cloud of dots. This visual simulation elicits an expanding radial motion, on which a lateral motion of dots is superimposed (leftward or rightward). The lateral motion was independent of both radial flow and steering control. As a result, subjects can control steering accurately from the radial flow, but steering is biased in the opposite direction to the lateral motion. This is consistent with the prediction based on the heading-perception bias rather than velocity summation. These results suggest that human control of steering utilises the output of heading-perception processing.

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BINOCULAR VISION, STEREO, DEPTH AND SPACE PERCEPTION

◆ **Does interpupillary distance predict stereoacuity for normal observers?**

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Interpupillary distance (PD) contributes to the size of binocular disparities. It seems reasonable to assume therefore that stereoacuity should be a function of PD, although no allowance is made for this possibility in most clinical stereotests (Lang et al, 1991 *Graefe's Archive of Clinical Experimental Ophthalmology* **229** 115–118). As far as we are aware the assumption that stereoacuity should be related to PD has not been tested by investigating whether PD correlates with individual differences in stereoacuity. We have done this by measuring the stereoacuities of one hundred and nine university students who satisfied the following inclusion criteria: no history of strabismus or amblyopia, better than 0.2 logMar (6/9.5) for each eye with correction if any worn, and either orthophoria or a well-controlled phoria. Stereoacuities were measured with a modified Howard–Dolman (H–D) apparatus, with viewing distance of either 5.5 m or 4.93 m,

to provide an accepted stereoacuity measure, and also with a new distance clinical stereotest under evaluation—the FD2 (Frisby–Davis Distance Stereotest; www.frisbystereotest.co.uk). PDs were measured with a PD-82II Digital PD Meter (Towa Medical Instruments Co. Ltd) and ranged from 53 to 69 mm, mean 60.3 mm. H–D stereoacuties ranged from 1.5 to 12.2 s of arc, mean 5.3 s of arc. The FD2 stereoacuity range was 4–40 s of arc, mean 11.4 s of arc. There was a low but significant correlation ($r = -0.27$, $p < 0.005$) between PD and H–D stereoacuity that could not be explained by gender. This result confirmed predictions but it is too weak a correlation to be clinically significant. It is unsurprising that it was not picked up by the FD2 stereoacuity test, whose test procedures satisfy clinical time constraints that entail less good resolution than those provided by H–D scores.

◆ **Stereomotion processing in human superior occipital cortex**

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Stereomotion (SM) is motion-in-depth produced by disparity changes. We have found a complex of brain areas involved in long-range stereomotion processing. How distinct is this SM-complex from that for lateral motion? In this study, we used fMRI to focus on a non-retinotopic area in the intra-occipital sulcus (IOS), which we have found to give one of the strongest responses to SM. In experiment 1, stereomotion, seen as backward/forward motion in depth, was generated by dynamic autostereograms. It was contrasted with stationary stimuli. In experiment 2, the same stimuli were used, but observed non-stereoscopically, thus producing lateral motion instead of stereomotion. In this way the monocular-motion images in experiments 1 and 2 were identical. In experiment 3, stereomotion was contrasted directly with lateral motion at the horopter. fMRI responses were obtained on a GE Signa 3T scanner with spiral acquisition in 26 axial slices, 4 mm thick, at 3 s TR through occipital, temporal, and most of posterior parietal cortex. Test and null stimuli alternated for 9 s each in 36 blocks per scan. The target IOS area was strongly activated in both motion/static contrasts (experiments 1 and 2). Does this area represent (a) a generic motion module, processing any retinal motion regardless of its depth interpretation, or (b) an area coding locally for azimuthal direction of motion, and hence specifically activated by every motion direction? Experiment 3 demonstrated surprisingly high activity in the same region, thus suggesting a distinct SM-selective neuronal subpopulation within the non-retinotopic portion of the IOS. The results revealed a stereomotion-specific activation in the IOS in superior occipital cortex, and they may also contribute to the understanding of the organisation of overlapping functionally distinct neuronal subpopulations.
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◆ **Are stereo and motion information to 3-D structure linearly combined?**

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In this study we investigated whether motion and stereo information to 3-D structure are combined in a linear fashion as predicted by most of the theories of cue combination. Observers binocularly viewed a motion and stereo specified random-dot planar surface. The observers' task was to place a probe dot on the perceived surface. The perceived position of the probe dot could be adjusted by modifying (i) its 2-D velocity, (ii) its binocular disparity, and (iii) a combination of the two, with respect to the planar surface. In different conditions we varied the relative intensity of the velocity and binocular disparity of the probe dot. If the hypothesis of linear combination of motion and disparity information is correct, then settings derived from different relative intensities of motion and disparity information must lie on a straight line in the velocity–disparity space. The results, however, show that this is not the case. This suggests that motion and stereo modules of 3-D shape reconstruction are not independent.

◆ **Evidence of strong coupling between stereo and shading information to 3-D surface reconstruction**

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Most theories of cue combination in 3-D shape perception postulate a modular organisation of the visual system. According to these theories, several independent modules estimate 3-D properties from different sources of information. The outputs of these modules are then combined in a statistically optimal fashion by a maximum-likelihood estimator (MLE). In this empirical investigation, we studied whether the MLE model of cue integration can predict how stereo and shading information are combined. The observers' task was to place a stereo-viewed

probe dot on a spherical surface that in three different conditions could be specified by (i) stereo shading, (ii) stereo-viewed random dots, and (iii) both cues combined. The MLE rule of cue integration predicts that the standard deviation (SD) of the observers settings in the 'combined cues' condition is smaller than each of the SDs in the 'stereo shading only' and 'random-dots only' conditions. Moreover, according to the hypothesis of independent modules, the predicted 'combined-cues' SD represents a lower bound of observers' uncertainty. Surprisingly, the results of this investigation show that the SD in the 'combined-cues' condition is well below (between 20% and 30% less than) the SD predicted by the MLE rule. These findings therefore indicate that shading and disparity information are not processed by independent modules.

◆ **Measuring HMD misalignment with interocular transformational apparent movement**

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If the displays of a binocular head-mounted display (HMD) are not directly in front of the eyes, the resulting misalignment increases the effort needed to maintain the binocular fusion. Consequently, the users may experience eye strain and other sickness symptoms. To decrease misalignment and the resulting eye strain, a method for display misalignment detection could be used. Here, the hypothesis was that interocular apparent movement might be used to detect the binocular distortion caused by the misalignment. To test the apparent movement method, the subjects' ability to detect interocular differences in the vertical and horizontal sizes of the half-images was compared. The first experiment was a temporal 2AFC experiment in which the subjects viewed stereoscopic images and decided which time interval contained three-dimensionally distorted image. The second experiment was a temporal 2AFC experiment in which the shapes were presented as an interocularly flashing sequence and the task of the subjects was to detect the display interval that contained more apparent movement. The results show that subjects detected the apparent movement more accurately than 3-D distortion. The results indicate that gradual distortions caused by the misalignment are more difficult to detect with the shape-detection method than with the apparent-movement method. Consequently, interocular apparent movement seems to be a better alternative for HMD misalignment detection and measurement.

◆ **Visual control of epipolar constraint by vertical size disparity**

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We examined whether vertical size disparity associated with an eccentric gaze direction can be used as epipolar constraint in stereo matching, reducing the search for corresponding features to a 1-D search along an epipolar line. We synthesised a variant of autostereogram in which an inclined surface about a horizontal axis emerges when stereo matching occurs along epipolar lines implied by eccentric viewing. The autostereogram was surrounded by a frontoparallel annulus consisting of random dots with overall size disparity, of which the vertical component is relevant to gaze eccentricity. We found, using this stimulus configuration, that observers perceived the inclined surface in the central region when vertical size disparity in the surround was consistent with the gaze eccentricity simulated in the autostereogram, demonstrating that stereo matching occurred along the epipolar lines implied by vertical size disparity. We also found that they instead perceived a slanted surface about a vertical axis in the central region when inconsistency was introduced in the simulated gaze eccentricity between the centre and the surround, indicating that vertical size disparity only imposed the global induced effect on the autostereogram whose stereo matching was established as zero-disparity. These findings suggest that vertical size disparity can function as epipolar constraint and may provide a relatively narrow search zone for stereo matching.

◆ **Orientation bandwidths of cyclopean channels measured with the use of notched noise**

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The spatial frequency bandwidths of cyclopean channels, responding to depth variations defined by binocular disparity, were measured by masking experiments and estimated to lie between 1–3 octaves (Cobo-Lewis and Yeh, 1994 *Vision Research* **34** 607–620). Here, a notched noise procedure was used to measure the orientation bandwidth of these channels. Thresholds were measured for the detection of sinusoidal depth modulations of a random-dot stereogram, either in isolation or in the presence of a disparity mask. Thresholds were measured for both horizontal and vertical modulations. The mask was formed from two samples, each the sum of a number of sinusoidal depth variations covering a 10° range of orientations. The orientation ranges of the two samples were positioned symmetrically around the signal, leaving a gap (notch) around the signal of between $\pm 10^\circ$ and $\pm 80^\circ$. Signal detection thresholds were measured for each notch

size, while the magnitude of the noise was held constant. Threshold elevation relative to the unmasked condition decreased as the size of the notch increased. Threshold elevation as a function of mask amplitude was also measured for masks centred on the signal orientation, allowing the orientation bandwidth of the channels to be calculated. The bandwidth (half-width at half-height) was estimated to be around 35° , for channels tuned to both horizontal and vertical orientations. These results are considered in relation to the suggestion that different areas of spatial summation underlie the detection of different orientations of cyclopean stimuli (Tyler and Kontsevich, 2001 *Vision Research* **41** 2235–2243).

◆ **Anisotropic property of stereoscopic vision**

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How accurately can we reproduce real depth in stereoscopic vision? In the present study, 3 objects (cylindrical shape, 21 cm in diameter, 20 cm in height)—A, B, X—were presented in the horizontal plane 40 m in depth, 21 m in width. Objects A and B were fixed at points A (0, 4 m, 0) and B (0, 14 m, 0), and object X was variable in location. These three objects were photographed from two different locations L (−3 cm, 0, 92 cm) and R (3 cm, 0, 92 cm) with a digital camera (Nikon D100, $f = 42$ mm) and images were projected on the screen stereoscopically with polarised filters. Subjects (seven males and eight females) observed binocularly stereoscopic images with polarised glasses at the distance of 3.5 m and judged the distance ratio AX/AB and the angle BAX once. The physical distance ratio AX/AB was 0.4, 1.0, 1.6, 2.2, 2.8, and the physical angle BAX was 0° , -4° , 4° , -8° , 8° , -12° , 12° , -16° , 16° , -20° , 20° . Object X was placed totally at 54 locations. Distance and angle data were averaged over the subjects and symmetrised laterally. As a result, it was found that (i) distance judgments were affected by the angle BAX, and perceived distances were longer than physical distances for the larger angles BAX, and (ii) angle judgments were affected by the distance AB, and perceived angles were larger than physical angles for the longer distances AB. This result implies that stereoscopic space is anisotropic. Furthermore, a stimulus configuration was reproduced from the result of distance and angle judgments. It was found that the physical geodesics was perceived to be curved to the outside in stereoscopic vision.

◆ **Cortical neuronal connections related to the 3-D reconstruction of visual space**

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The geometry of visual scene projection onto the retinae and the pattern of decussation in the visual pathway determine the necessity of binding and convergence of inputs from the two eyes to the visual hemifields for depth discrimination. We investigated the distribution of retrogradely labelled cells in cortical areas 17, 18 in the cat after microiontophoretic horseradish peroxidase (HRP) injections into the single cortical columns of area 17, 18, 19, or 21a. We have shown the clustered pattern of intrinsic labelling and asymmetric location of labelled callosal cells which was associated with the specific pattern of labelling in layers A and A1 of lateral geniculate nucleus. These data suggest that intrinsic and callosal connections are eye-specific and may provide for each eye the separate binding of two visual hemifields. Preliminary data show that pattern of callosal connections has not changed in strabismic cats. After HRP injections into columns of area 19 or 21a the disparate inputs from areas 17, 18, and transition zone 17/18 were revealed. Such connections may provide the local depth information and the selection of stereoscopic surfaces in central sectors of visual space.

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◆ **Eye position influences contrast responses in V1 of alert monkey**

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Do our cells in V1 respond differently when we look in different places? In order to answer this question, we studied neuronal responses to moving bars in V1 of an alert monkey viewing the bars from different eye positions. The monkey was trained to fixate on an LED attached to the screen placed in three positions: straight (0°), 10° to the right (10R), or 10° to the left (10L) in the horizontal plane. We recorded contrast responses in 21 cells. Changing eye positions significantly influenced the amplitude of the response in 17 cells. In 7/17 cells in the 0° position, in 5/17 cells in the 10R position, and in the remaining 5/17 cells in the 10L position, responses were larger than in the other two positions. We fitted contrast responses $r(c)$ with the Naka–Rushton equation: $r(c) = R_{\max} [c^n / (c^n + c_{50}^n)]$, where R_{\max} is the maximum response, c is the contrast, c_{50} is

the contrast at the half of R_{\max} , and n is nonlinearity. We analysed only those responses with a sufficiently good fit (estimated by the RMS). In most cases changing the eye position had small influence on n , but significant influence on R_{\max} and c_{50} . We analysed 18 contrast responses to increment and decrement bars. R_{\max} changed, by more than 20%, in 12 cases, and c_{50} in 14 cases. In 10 measurements, both R_{\max} and c_{50} changed as the eye position changed. Our preliminary data also suggest that the eye position could differently influence the size of the increment and decrement zones in the classical receptive field of V1 cells.

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◆ **Spatiotemporal frequency tuning of two channels for stereopsis**

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It has been suggested that more than one channel with different spatiotemporal frequency tunings contribute to stereopsis. We estimated spatial-frequency tuning of two possible channels sensitive to binocular disparity from contrast threshold with various disparities for depth discrimination at a number of spatiotemporal frequency conditions. The stimulus display consisted of four squares arranged in a 2×2 array with gaps to separate them. Each square was filled with vertical sinusoidal gratings. The observers responded which of the diagonal square pairs appeared to be closer in depth. A staircase procedure was used to obtain contrast threshold as a function of phase disparity for each combination of six temporal frequencies (0.15–20 Hz) and three spatial frequencies (0.23–3.75 cycles deg^{-1}). Contrast sensitivity peaked at about 0.078 cycle in phase disparity for stimuli with high spatial and low temporal frequencies and at about 0.188 cycle for stimuli with low spatial and high temporal frequencies. The peak phase disparity for other conditions ranged somewhere between the two values. We assumed that two mechanisms with these peak sensitivities contributed to the measurements and determined the contrast sensitivity in each condition with the sensitivity functions of the two mechanisms. A least squares method was used to find the contribution of each mechanism to the best fit at each spatiotemporal frequency. Since the two-channels mode predicted our data well, we conclude that there are at least two mechanisms with different spatiotemporal frequency tuning in stereopsis.

◆ **Activity in human prefrontal cortex for volume perception with binocular viewing**

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One of the greatest mysteries in cognitive science is the human ability to perceive visually presented objects with high accuracy and lightening speed. The neural substrates of our innate ability to perceive and identify objects remain elusive. Volume perception is one of the important issues in the study of human visual perception. In this perception, objects are perceived as solids which occupy closed spaces. Several years ago, a new visual effect named the mime effect was reported (Zhang et al, 1998 *Japanese Journal of Applied Physics* **37** L329–L332), in which an illusory 3-D volumetric object is perceived with binocular viewing due to some stereoscopically displayed inducing objects. Here we report our fMRI measurement of brain activities for volume perception by applying the visual stimuli in the mime effect. We compared brain activity between the condition when the subjects perceived a 3-D volumetric object and that for attaining 2-D perception, and found that the volume perception involved a large range of the visual cortical areas. Besides activity in the lower occipital visual cortex, activities in some high-level cortical areas in the parietal and anterior lobes were also observed. In particular, the right prefrontal cortex was more activated when the subjects attained volume perception. This shows that the prefrontal cortex also takes part in the visual processing of a complex visual stimulus such as volume perception in the mime effect.

[The fMRI experiments were conducted at ATR Brain Activity Imaging Center.]

◆ **Function of binocular unpaired regions on illusory volume perception**

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Transparent illusory volume perception from plural objects arranged in three-dimensional space with binocular viewing was reported (Zhang et al, 1998 *Japanese Journal of Applied Physics* **37** L329–L332). We tried comparing two kinds of binocular unpaired regions in this phenomenon. One was the binocular unpaired regions arising from inter-object occlusion (UI), and the other was the binocular unpaired regions arising from self occlusion (US). In this psychophysical

experiment, four types of stimuli were produced by varying the properties of objects arranged on an imaginary sphere: (i) stimulus that provided both UI and US, by drawing each object as lined solid that was opaque; (ii) stimulus that provided neither UI nor US, by drawing each object as wire frames so that the rear side was seen through; (iii) stimulus that provided only US, by arranging the opaque objects of lined solid so that they would not hide any part of another object from observer's view; and (iv) stimulus that provided only UI, by replacing objects which provided US in stimulus (i) with wire-frame objects. In each stimulus, we measured the perceived volume of the imaginary sphere. The results indicate that both UI and US could facilitate the volume perception, but US is more effective. We suggest that the visual system has the function to modulate the depth scale of the imaginary sphere as a global structure, using US of each object as a constituent element.

◆ **Interocular contrast-ratio modulation spatial frequency influences the 'Venetian blind' effect in irradiation stereoscopy**

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Two dichoptically presented squares that are geometrically identical but with different luminances will appear to be rotated out of the frontoparallel plane (Cibis and Haber, 1951 *Journal of the Optical Society of America* **41** 676–683). The bars of a dichoptically presented pair of square-wave gratings will appear to rotate about their individual vertical axes when one of the gratings has either a reduced luminance or contrast (Filley and Stine, 1998 *Perception* **27** Supplement, 99; Stine and Filley, 1998 *Perception* **27** Supplement, 106). While neither the spatial frequency of the square-wave grating nor the width of the blur of the bars of the grating seems to influence threshold luminance or contrast ratios to see a rotation with achromatic stimuli (Khutoryansky, 2000 *Influence of Blurry Edges on the Venetian Blind Effect* unpublished Masters thesis, University of New Hampshire), increasing the width of the blur of the bars of the grating lowers threshold contrast ratios when there is a dichoptic cone-contrast difference between the gratings (Stine et al, 2001 *Perception* **30** Supplement, 74). In three experiments involving three subjects each, we varied the spatial frequency of the interocular contrast-ratio modulations of 4.0 cycles deg⁻¹ (experiments 1 and 3) and 6.6 cycles deg⁻¹ (experiment 2) square-wave gratings. Interocular contrast-ratio thresholds to induce the effect were measured. In experiments 1 and 2, thresholds to perceive a rotation dropped with the spatial frequency of square-wave interocular contrast-ratio modulations over the range of 0.33 cycle deg⁻¹ to 3.3 cycles deg⁻¹. In experiment 3, thresholds also dropped with spatial frequency when a sine-wave interocular contrast-ratio modulation was used. For two of the three subjects, the threshold for the square-wave modulation was less than that for the sine-wave modulation at low spatial frequencies. We discuss these results with respect to monocular contrast discrimination and binocular interactions in contrast perception.

◆ **Monocular texture segregation and proto-rivalry**

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Orientation-defined texture boundaries that would be erased by binocular fusion nonetheless remain detectable in brief dichoptic exposures (Kolb and Braun, 1995 *Nature* **377** 336–338). However, orientation-defined search is impossible when the right eye's target is the left eye's distractor, and vice versa (Wolfe and Franzel, 1988 *Perception & Psychophysics* **44** 81–93). Were different element densities responsible for the qualitative difference between these results? In our first experiment, we created monocular texture boundaries, which would be erased when binocularly fused, by using orthogonally oriented Gabors. Observers required less than 250 ms to find these boundaries when the Gabors were arranged on a 24 × 24 grid. More than 1 s was required for a 16 × 16 grid covering the same area. Producing the same result was a second experiment, in which each eye's Gabors alternated in position on the notional grid, thereby revealing the texture boundary to high-level analysis. Also, when all Gabors in the second experiment were presented to each eye binocularly, as opposed to dichoptically, observers required more than 1 s to find the boundary, regardless of density. These results suggest dense arrays are required for monocular texture segregation, but point-wise competition between the eyes is not. Dichoptic stimuli that cause rivalry in long exposures are often described as being fused in short exposures, but our experience is more consistent with that of transparency. We easily discriminated between dichoptic and binocular plaids in exposures as short as 20 ms, even when contrast was randomly perturbed. Monocular texture segmentation can accompany this apparent transparency, which we term 'proto-rivalry' that is distinct from true binocular fusion and rivalry.

◆ **Similar contrast effects for motion and colour during binocular rivalry**

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Two dichoptically presented, dissimilar stimuli will engage in binocular rivalry. Which of the two stimuli dominates the percept can be affected by a surrounding stimulus, as has been shown by Fukuda and Blake for orientation (1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 362–370). To investigate whether this phenomenon can be generalised, we now extend the experiments to the motion and the colour domain. Two discs containing a leftward moving grating in one eye and a rightward moving grating in the other eye were presented at the centre of fixation. The discs could be surrounded by an annulus that contained motion in the same direction as one of the two discs. The annulus was presented to only one of the two eyes. The direction of motion of the annulus could either be that of the disc that was presented to the same eye, or that of the disc that was presented to the other eye. Observers continuously indicated the perceived direction of motion of the central disc. We found that the disc that contained the motion direction opposite to the surround was more dominant, irrespective of its positioning (same or different eye as compared to the annulus). We ran the same experiment in the colour domain; that is, instead of leftward and rightward moving gratings, we now had a red disc in one eye and a green disc in the other eye. The discs as well as surrounding annuli were made isoluminant relative to a yellow background. The disc with the colour opposite to the surrounding annulus was more dominant, irrespective of its positioning. We have observed similar contrast effects during rivalry in both colour and motion. Moreover, these contrast effects occurred irrespective of the position of the surround, suggesting that the mechanism behind these contrast effects is at least partly binocular.

◆ **Monocular and binocular contribution to motion contrast**

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Two gratings moving in opposite directions, presented to different eyes will result in binocular rivalry. We have shown previously (Paffen et al, 2003, VSS03, Abstract FR 117) that when a surrounding annulus moving in the same direction as one of the gratings is presented, the grating moving in the opposite direction dominates the percept. Here, we investigate to what extent monocular and binocular mechanisms contribute to this phenomenon. A disc containing two oppositely moving vertical sine-wave gratings was presented monocularly. By varying the contrast ratio of the gratings, motion energy was varied between leftward and rightward motion. We measured psychometric curves for discriminating leftward from rightward motion for the central disc for different surround-conditions: in the baseline condition, a surrounding annulus containing a stationary grating was presented to either the same eye as the disc or to the other eye. In the experimental condition, an annulus containing motion in the same direction as one of the components of the disc was presented to either the same eye as the disc (same-eye surround; monocular condition) or to the other eye (other-eye surround; binocular condition). In both the monocular as well as the binocular condition, we found a significant shift in perceived direction of motion towards a direction opposite to that of the surround. This shift, however, was much larger in the monocular surround-condition. Thus, both monocular and binocular mechanisms contribute to motion contrast effects during binocular rivalry.

◆ **Eyedness: An optometric approach**

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Eyedness, the fact of a preferred or dominant eye, is usually determined by a questionnaire or a simple sighting task (card test). This task requires binocular and monocular alignment of a target through a hole in the middle of a card; the eye that is collinear with the hole and the target is revealed as the sighting-dominant eye. We have compared these coarse accounts of eyedness with various optometric tests of binocular functions within a sample of one hundred and three subjects (aged between 19 and 51 years; thirty-five female, sixty-eight male). The tests included visual acuity and accommodation in each eye, stereo dominance (perceived left or right position of physically aligned stereo images; Polatest, Zeiss), dominance due to binocular rivalry and fixation disparity (Mallett test). Sighting dominance (card test) was leftward in 32% and rightward in 68% of the cases and was highly correlated (Kendall's $\tau_b = 0.70$) with eyedness, assessed by a German adaptation of Coren's questionnaire (identical eye preferences, except for nine subjects of which seven were ambilateral). Further significant associations were restricted to

stereo dominance which correlated with sighting dominance ($\tau_b = 0.55$), questionnaire data ($\tau_b = 0.50$), and rivalry dominance ($\tau_b = 0.28$). Thus, eyedness as assessed by questionnaire is closely related to sighting dominance, and both measures are related to stereo dominance. Conversely, eyedness appears to be fairly unrelated to dominance concerned with binocular rivalry or acuity.

◆ **Binocular processing models for luminance and colour at isoluminance variations**

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We analysed how monocular visual reaction times (VRTs) are combined to provide the binocular VRT, using the standard modelling techniques for co-activation and parallel race models (Miller, 1982 *Cognitive Psychology* **40** 331–343; Grice et al, 1984 *Perception & Psychophysics* **35** 451–463; Hughes and Townsend, 1998 *Psychological Science* **9** 53–60). We measured VRT for luminance and colour at isoluminance variations (L&M-constant cone axis and S-constant cone axis according to Boynton's two-stage colour-vision model). Circular random stepwise stimuli were presented on a colour monitor at a 2-deg field size. A 15 cd m⁻² achromatic reference stimuli were selected to provide suprathreshold luminance and colour at isoluminance variations. In this latter case, the hue-substitution method (Nissen and Pokorny, 1977 *Perception & Psychophysics* **22** 457–462) was used. For this arrangement, manual simple VRTs were measured at the fovea under monocular and binocular observational conditions. Two human observers took part in the experiment. Upper and lower parallel race bounds were calculated by using the cumulative probability functions. The Savitzky–Golay smoothing technique was followed to avoid random fluctuations. At the same time, the range of the binocular capacity coefficient was estimated to reinforce the above analysis. The results for all observers confirm that neither the standard parallel race nor co-activation models can take into account the binocular data in the context-independent hypothesis for both luminance and chromaticity at isoluminance variations.

◆ **Perceptual distortion: Interaction between 3-D illusory surfaces**

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One of the authors reported the occlusion and intersection phenomena between 3-D illusory surfaces in stereoscopic display (Idesawa, 1991 *Japanese Journal of Applied Physics* **30** L751–L754; 1992 *Artificial Neural Networks* **2** 561–564). We investigated distortion perception in which one or both illusory surfaces were distorted by the others. Specifically, we observed the perceptual properties of distortion induced by the interaction between two illusory rectangular surfaces using cross-configuration of them. We performed two kinds of observations: orientation dependence, and interpolation or supporting-length dependence. In the former kind, -90° to 90° with 5° steps orientations of cross-configuration were examined; in the latter kind, different lengths of illusory rectangle or supporting part (disparity part) at 45° (135°) orientations were tested. The results showed that distortions were perceived at any orientation in the illusory cross-configuration, while distortions were observed only at 0° or 90° orientation in the real cross-configuration. Surprisingly, both illusory rectangles could be distorted simultaneously almost at any orientation (saddle distortion); one of illusory rectangles nearer to the horizontal orientation was easier to distort than that nearer to the vertical direction. Moreover, the illusory rectangle with longer supporting length was more difficult to distort, while illusory rectangle with longer interpolation span was easily distorted. Our view is that distortions are induced on both illusory rectangles, since there is no disparity in the cross area. Furthermore, we infer the existence of perceptual rigidity which is similar to the beam theory in the real world (bending characteristic of beam).

◆ **New phenomena on depth perception of moving dots obeying the rotation reversals of Ullman's cylinder**

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Human visual system can perceive 3-D structure from 2-D motion. Sinusoidally moving dots were produced by projecting orthogonally a vertical rotating transparent cylinder with randomly distributed dots stuck to it. We can easily perceive rotating cylindrical structure from the dots; however, because of the lack of depth cue for two groups of oppositely moving dots, perceptual rotation direction of the cylinder often reverses. This has been referred to as the Ullman's cylinder (Ullman, 1984 *Perception* **13** 255–274). In addition, depth difference could be perceived

between two layers of oppositely moving random dots with a horizontal component (Imamura, 1997 *Sensing and Perception* **4** 65–75). By providing flank areas with uniformly moving dots on both sides of the projected cylinder, we observed the depth of moving dots in the flank areas. We found that the depth of moving dots in the flank areas was reversed synchronously with the reversals of the direction of rotation of the perceived cylinder. Moving dots in the flank area with the same moving direction as that of the nearer dots on the cylinder were perceived as being nearer, while the dots moving in the opposite direction, ie the same direction as that of more remote dots on the cylinder, were perceived as being further. The perceptual depth difference of flanks in the two conditions of the rotation directions was measured by us with illusory depth probe stimuli in binocular viewing. The overall results confirm that there is a perceptual depth difference of moving dots in the flank area in the two perceptual conditions of the direction of rotation of the cylinder.

◆ **Surface slant information affects perception of pictorial images**

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When viewing a pictorial image, the retinal projection is consistent with the portrayed scene only when the image is viewed from the centre of projection (COP). We generally do not view pictures from this position, yet the perceived layout is mostly unaffected. Possible explanations are: (i) information about the slant surface of the picture is used to correct for the obliqueness of viewpoint relative to the COP; (ii) geometric information available in the pictorial image (eg vanishing points) is used to recover the COP and correct for oblique viewing; (iii) no actual visual compensation occurs; instead, prior assumptions about rectangularity, symmetry, and other object properties determine the percept. Stimuli were realistic ray-traced images of a scene containing ellipsoids. Observers indicated whether a target ellipsoid appeared narrower or wider than a sphere while viewing the images obliquely on a CRT. The slant of the CRT was varied, and slant information was controlled in four conditions: monocular viewing through an aperture, monocular viewing with the CRT frame visible, binocular viewing through an aperture, and binocular viewing with the frame visible. Consistent with the first explanation, the amount of slant information available had a large and predictable effect on observers' settings. The third explanation can be ruled out because all retinal images specified similar plausible 3-D interpretations, namely ovoid objects. The second explanation can also be discounted because the images were always viewed from the COP, and any available perspective information would indicate that no correction of viewpoint is necessary. Our results suggest that compensation for obliqueness of view is accomplished by measuring the slant of picture surface relative to the line of sight.

◆ **Three-dimensional object discrimination after rotation in depth in a natural scene: Spatial-frequency-relevant information**

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The human visual system can recognise objects from varied images, whether different in point of view, lighting (luminance, chromatic content), or detail level. The influence of spatial-frequency content on the visual recognition of a target has been previously studied (Giraudet and Roumes, 2001 *Perception* **30** Supplement, 26). Object-perception theories point towards structural description (Biederman and Gerhardstein, 1993 *Journal of Experimental Psychology: Human Perception and Performance* **19** 1162–1182) with a predominant role of high spatial frequencies in discrimination (Uttal et al, 1995 *Perception & Psychophysics* **57** 668–681). We investigated physical characteristics of objects and their spatial organisation leading to correct perception in a natural scene, despite various aspects. Three objects, seen from three points of view in a natural environment, made up the original images considered in this study. Test images were a combination of spatial-frequency-filtered original images and an additive contrast level of white noise. The observer's task was a same-versus-different forced choice with spatial alternative. Test images had the same noise level in a presentation sequence. Discrimination threshold was determined by modifying the white-noise contrast level by means of an adaptive method. The resulting threshold thus obtained sheds some light on the capacity of the human visual system to recognise objects under different physical descriptions (spatial-frequency content, orientation in depth).

◆ **Size constancy in near and far visual space**

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Binocular perceptual cues are commonly thought to be among the most important optical sources of information necessary to achieve size constancy. What happens when we observe objects in the distance where the efficiency of these cues sharply drops? In order to test size constancy for different distances (2–10 m), we conducted a relative-size-judgment experiment where two stimuli were presented to an observer at the same viewing distance, but in mutually different orientations. Observers binocularly viewed a stimulus defined by four red LEDs lying on the ground surface, and their task was to match the lengths of two opposite intervals. Both intervals were crossed in the middle of their length; therefore, in the case of a correct answer, the four dots formed a rectangle. We have found that the influence of orientation is not constant across all viewing distances studied. Whereas judgments of the observers were independent of relative orientations at the distance of 2 m, the latter became a critical factor as the distance of the stimuli was increased. The accuracy and reliability of judgments at greater distances linearly decreased with increasing difference between orientations, indicating the determining role of retinal size information.

◆ **Judging three-dimensional circular shapes for measuring the perception of shaded surfaces**

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Some properties of our three-dimensional world are not easy to derive from the retinal input due to the dimensionality reduction inherent in the mapping of a three-dimensional world onto two-dimensional sensors. We describe a Bayesian model that is able to incorporate the combination of prior shape assumptions with additional information about depth (ie information about the orientation of the shape towards the observer) as a solution for this problem. We then propose to fit a two-parameter version of the model to a set of shape inferences made by real observers. The two parameter values defining the model that best simulates this set of inferences will give us an idea about the perception of the orientation of these shapes towards the observer. In the first experiment, using very simple elliptical shapes projected on the surface of a real sphere, we asked our observers to categorise these shapes as being a circle painted on the surface of the sphere or not. We found that the parameters of the best-fitting models change systematically according to the manipulation of the additional information about depth: both the mean and the standard deviation of the underlying orientation distributions change with the slant of the underlying surface. In the second experiment we asked our observers to make the same set of inferences, thus keeping the task the same as in the first experiment, but changing the viewing conditions (categorising the same shapes projected on the surface of a photograph of the sphere). This time the underlying orientation distributions showed a shift towards the frontoparallel plane, in line with results of previous studies in which the same kinds of stimuli but another kind of task were used.

◆ **Motion-in-depth aftereffect following adaptation to contrast change**

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Contrast is a cue for depth perception; a near object has high contrast and an object located at far distance has low contrast. What happens if the contrast of an object varies in time? Do we perceive the object moves in depth? We examined whether contrast change produces motion-in-depth perception by measuring the motion-in-depth aftereffect. The adapting stimulus was a circular sine-wave grating of 1 s duration whose phase was reversed at every 250 ms. The contrast of the gratings increased or decreased. The test stimuli were also circular sine-wave gratings of 1 s duration whose phase was shifted with various angles at every 250 ms. The amount of the shift below (over) 180° produced expanding (contracting) apparent motion. The subjects judged whether the test stimulus appeared to move towards or away from them. We measured the null point (the angle of the phase shift that produced perception of no motion-in-depth). After adapting to decreasing contrast, looming aftereffect was observed, and after adapting to increasing contrast moving-away aftereffect was observed. The results indicate that contrast change produces motion-in-depth perception, suggesting that the human visual system integrates the contrast information to achieve depth perception.

◆ Pedestal depth discrimination of contrast-windowed patterns

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Binocular matching of patterns is aided by applying a shifted contrast window to the patterns. We sought to understand whether the contrast window facilitates binocular matching by (a) simply changing the energy spectrum of the image, or (b) enabling a window-extraction process. In the first case, binocular matching can be performed by first-order filtering. In the second case, binocular matching requires a second-order window-extraction process. In the experiments, we manipulated the type of contrast windowing so that it would pose varying degrees of difficulty for window extraction, yet have a minimal effect on the spectrum of the images. This was done by using a sharp-contrast window for easy extraction and a cosine window for difficult extraction. We also manipulated the spatial frequency of the contrast-windowed random-noise patterns. Observers performed a pedestal depth discrimination task. We found that the type of windowing had a large effect on performance, even though the energy spectrum of the images was very similar. The effect of spatial frequency was absent for the sharp-contrast window, but was evident for the cosine window. We conclude that binocular matching in the human visual system uses both linear filtering and a second-order window-extraction process.

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◆ The role of the elevation cue in pictorial depth space

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It is widely accepted that the relative height of objects is an important cue of depth perception in pictorial displays. However, this phenomenon has never been investigated experimentally. The present study was designed to systematically test the elevation cue in various pictorial contexts. An experiment was conducted to examine the role of relative elevation of two identical $1.43 \text{ deg} \times 1.43 \text{ deg}$ squares presented with different orientations to one another (at 45° and 225°) and at different separations from one another (1.43 deg and 2.86 deg) in the perception of depth. In addition, the two squares were presented at seven different heights, on the left and on the right of the monitor and within different pictorial contexts (eg a gradient on the floor only; gradients on the floor limited by a wall at a distance; gradients both on the floor and ceiling limited by a wall at a distance; and a single line of the horizon), together with a control condition without any background structure. As expected, the results show floor gradient effects in the perception of depth as a function of relative elevation. In addition, the wall and the ceiling gradient significantly change this effect. The depth effect is inverted, with squares in higher positions being perceived closer.

◆ Does a virtual reconstructed space lead to the same impression of depth as the natural space?

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We have studied the depth perceived in a natural space and the depth perceived in a virtual simulation. The virtual space was built on the basis of two monocular cues, linear perspective and photometric cues, and on the basis of geometrical disparity. The perceived depth was evaluated (i) verbally and (ii) with a probe (Tsai and Victor, 2000 *Vision Research* **40** 2265–2276) using binocular horizontal disparity. This binocular probe is composed of two vertical rectangles of random-dot stereograms, seen binocularly and located on both sides of the object to be localised. The disparity of the probe can be changed in order to equalise its apparent depth with the depth of the object tested [Monot et al, 2002 *Technique: La Vision des Oeuvres* (15) pp 76–82; Pichereau et al, 2002 *Perception* **31** Supplement, 125]. The investigation consisted of two parts: (i) verbal evaluation of the relative distance between two natural objects, (ii) evaluation with the probe of the relative distance (a) between these same objects and (b) between these same objects which have been simulated. This study, in natural space, revealed a difference between the true value and verbal estimation of relative depth and between the true value and the result of measurement with the probe, but no or little difference between verbal estimation and probe measurement. Furthermore, we have highlighted a difference between evaluations of relative depth in natural and virtual space when the binocular probe is used. Using this objective method, we have shown that the reconstitution of virtual space on the basis of monocular and binocular cues does not lead to the same ‘percept’ of relative depth.

◆ **The monocular, panoramic visual field**

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The monocular visual field is often said to be two-dimensional, by which is probably meant that the depth dimension is due to monocular cues. The visual field is phenomenally three-dimensional, though the depth dimension is special in the sense that visual rays are conserved. Indeed, one may conceive of mental transformations in this space, but these can only change the depth values in any direction, but not these directions themselves. This leads to a very specific non-Euclidian geometrical structure. I identify the group of congruences (proper motions) and similitudes of this space. There exist two distinct types of similitudes (in Euclidian space there is only one!), one that scales the depths and one that scales the visual angles. The former type is well known, the classical treatment is Adolf Hildebrand's 1893 *Das Problem der Form in der bildenden Kunst* 1893 [*The Problem of Form in Painting and Sculpture* translation by M Meyer, R M Ogden (1945, New York: G E Stechert)]. The latter type seems to have gone unnoticed. It has important applications though; for instance, it can be used to prepare minified representations of panoramic visual scenes that are fit to present in print. In the printed image, the visual angle at normal reading distance is much smaller than the visual angle subtended by a panoramic scene. This leads to the well known "distortions due to wide-angle lenses". Such distortions can be removed by using the present theory.

◆ **Parallelity under free viewing conditions**

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Visual space is deformed as compared with physical space. The structure of this deformation has intrigued many researchers. Most research has been done under restricted viewing conditions, eg dark rooms, head fixed, etc. Our goal was to gain insight in the structure of the deviations found without any restrictive viewing conditions. The experiment was done in an office environment with a parallelity task. The room was empty and the walls, doors, windows with closed blinds, etc were visible. In this task, a rod had to be rotated by using a remote control in such a way that it looked parallel to a reference rod. The two rods were placed at eye-height of the seated observer. We looked at three parameters, namely the separation angle, that is the visual angle between the two rods, the relative distance of the rods, and the orientation of the reference rod. Large deviations from veridical settings were found. The size of the deviations depended linearly on the separation angle. The relative distance had no effect on the deviations. The reference orientation had an effect for two out of four observers. Surprisingly, these results are comparable to the results obtained by Cuijpers et al (2000 *Perception* **29** 1467–1482) with the same task, but without the additional cues made available through walls, ceiling, and floor of an office room. So the extra amount of information present in our setup did not improve performance. Even in a relatively rich environment visual space remains deformed.

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◆ **Collinearity and exocentric pointing under free viewing conditions**

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Visual space is deformed as compared with physical space. The structure of this deformation has intrigued many researchers. Most research has been done under restricted viewing conditions, eg dark rooms, head fixed, etc. Our goal was to gain insight into the structure of the deviations found without any restrictive viewing conditions. The experiment was done in an office environment with the use of three tasks. Two of these tasks are discussed here, namely the collinearity task and the exocentric-pointing task. In these tasks, rods, placed at eye-height of the seated observer, had to be aligned with each other or made to point towards a target by means of a remote control. We looked at two parameters, namely the separation angle, that is the visual angle between the two rods, and the relative distance to the rods. Large deviations from veridical settings were found. For both tasks, the separation angle and the relative distance had an effect on the size of the deviations. It shows that visual space is deformed even in a setup where additional cues are available. When comparing the data of these tasks with data of a parallelity task, one can see that the deformation of visual space is not uniform for different tasks. So one cannot speak of a single visual space; the geometry of visual space is task-dependent.

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◆ **Shape perception in pictures: The effects of geometrical and grey-scale manipulations of 2-D renderings**

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Shape perception in pictures depends on available depth cues, eg occlusion, shading, texture gradient, etc. Moreover, viewing conditions and task to be performed by the observer for externalising the percept may influence the perceived shape of objects in 2-D renderings. In the present study, we used as primary set of stimuli six different grey-scale photographs of a torso. In each photograph, the pose of the torso was varied, but the rest of the scene was kept the same. We performed several manipulations on the photographs and investigated their influence on pictorial relief. Geometrical manipulation consisted of mirror-reflection and rotation: the primary set of six stimuli and their left–right mirrored versions were shown in four different orientations with orientation differences of 90°. Manipulation of image quality consisted of blurring: pictures were presented in ten different degrees of blurring. Grey-scale manipulation consisted of inversion: negatives of the primary set were shown. All stimuli were presented to a monocularly looking observer on a flat frontoparallel monitor screen, centred in the straight-ahead direction. The pictorial reliefs were measured by adjusting shape and orientation of an elliptical gauge figure superimposed on the torso at different locations. When a fit was achieved, the gauge figure looked as a circle painted on the pictorial surface. The probes were presented in random order, one at a time. The pictorial reliefs reveal significant differences that can be described by overall depth shears. These transformations can be interpreted as mental eye movements. The results show systematic influences of the diverse picture manipulations.

◆ **Effect of motion parallax on perceived size and perceived distance**

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We conducted two experiments to determine how motion parallax influences perceived size and perceived distance. Our experimental stimuli consisted of a standard (upper) circle, a comparison (lower) circle, and a horizontal line that indicated the horizon, which were displayed on a computer monitor. Subjects estimated the relative size and distance of the comparison circle compared to the standard circle. We conducted two manipulations of the degree of motion parallax: (i) Simultaneous manipulation of the ratio of vertical separation from the horizon, and the ratio of velocity between the comparison and the standard circles, which are always equal (c/s ratio); (ii) The absolute velocity of the standard circle. The motion parallax increases as the c/s ratio and the velocity of the standard circle increases. The purpose of our study was to examine the effects of these two variables on the estimation of size and distance. The results of experiment 1 indicated that both size and distance estimates of the comparison circle decreased as the c/s ratio increased, suggesting that motion parallax was veridically utilised for making these estimates. However, velocity did not influence these two estimates. The results of experiment 2 conducted with an expanded velocity range showed that the effect of the velocity of the standard circle had a significant effect for size estimates only. These results demonstrate that motion parallax is an important cue for the estimation of both size and distance; however, different information included in motion parallax may differentially determine size and distance estimates.

DEVELOPMENT AND AGEING, LEARNING, AND MEMORY

◆ **Judgments of taxonomic similarity among quasi-biological stimuli: Associations with age and reading ability**

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We investigated judgments of 'intuitive taxonomy' among quasi-biological stimuli, the 'caminalcules', using both printed pages and an electronic interface to elicit triadic comparisons ('Which two of these three stimuli are more closely related?'). Observer performance was assessed by comparing judgments against consensual and objective underlying patterns of dissimilarity. We examined perception at basic, subordinate, and superordinate levels by assessing the relevant triads separately. Observers were schoolchildren, varying in age and in reading ability relative to age. Both variables influenced performance, but in different ways, distinguishing between responses from youthful above-average readers and those from older below-average readers. The results suggest the involvement of at least three perceptual strategies in classifying unfamiliar complex stimuli.

◆ Development of asymmetry for the perception of expansion/contraction

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The human visual system has an asymmetry for the perception of expansion/contraction. Takeuchi (1997 *Vision Research* **37** 2083–2090) demonstrated that an expansion pops out from contracting distractors, whereas a contraction does not pop out from expansions. We examined the development of such asymmetry in infancy. In experiment 1, fifty infants, 2–8 months old, were exposed to an expansion-search stimulus. The expansion-search stimulus consisted of one expansion as a target and eleven contractions as distractors. Infants aged over 3 months showed a significant preference for the target, but 2-month-old infants did not show this preference. These results suggest that even 3-month-old infants can detect an expansion in a mixed expansion/contraction display. In experiment 2, fifty infants, 2–8 months old, were exposed to a contraction-search stimulus. The contraction-search stimulus consisted of one contraction as a target and eleven expansions as distractors. Results showed no significant preference in all infant groups. In experiment 3, we examined the spontaneous preference of infants for an expansion over a contraction. No preference for an expansion was shown. These results suggest that the difference between experiments 1 and 2 was not due to the spontaneous preference of infants for an expansion. Results of experiments 1, 2, and 3 suggest that the asymmetric response for the expansion/contraction detection emerges at 3 months of age.

◆ Perception of motion transparency in infants

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In order to perceive motion transparency, local paired dots moving in opposite directions need to be located 0.4 deg apart (Qian et al, 1994 *Journal of Neuroscience* **14** 7357–7366). We studied the development of the perception of motion transparency using these paired dots stimuli. All stimuli consisted of 200 dot movements, half of them rightward and the other half leftward. We prepared two types of stimuli: one was transparent-target motion and the other was distractor motion. In transparent-target motion, vertical distance between the dot moving rightward and the dot moving leftward was a minimum of 1 deg; in distractor motion, the separation was within 0.4 deg. We presented the transparent-target and the distractor motion side-by-side simultaneously. In one trial, stimuli were presented for a maximum of 5 s and a total of 16 trials was conducted on each infant. Two-alternative forced-choice preferential looking was used to determine whether infants see the transparent motion or not. Results demonstrated that infants 4 to 7 months old show statistically significant preference to the transparent motion, but infants 2 to 3 months old do not show this. These tendencies are independent of the dot size or dot speed. These results suggest that the perception of motion transparency emerges at the age of 4 months.

◆ Sensitivity for first-order and second-order motion in normal and strabismic children

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Psychophysical and physiological evidence suggests the existence of multiple processing channels for first-order and second-order stimuli (Clifford et al, 1998 *Brain Research* **6** 263–271). Measures of contrast threshold in the elderly show a larger increase for the detection of second-order stimuli (Habak and Faubert, 2000 *Vision Research* **40** 943–950). Atkinson et al (1993 *Investigative Ophthalmology & Visual Science* **34** 1357) report that infants aged 8 to 20 weeks prefer the first order without variation in sensitivity. The purpose of this study was to test if there is a difference in maturation of first-order and second-order motion. Stimuli were generated with Vpixmap[®] software and were based on those of Ledgeway and Smith (1994 *Vision Research* **34** 2727–2740). One hundred and sixty-one children 0.67 to 7 years old participated in the experiments: seventy-three normal, forty-eight strabismic, and forty pre-term. A forced-choice preferential looking procedure was used to measure the minimum contrast necessary to evoke a preferential looking behaviour for both types of stimulus. Log thresholds for motion varied linearly as a function of the log age in the control population and showed the same profile of maturation for the two stimuli. The contrast threshold for second-order motion was 10 times higher in all groups of infants with large inter-individual differences. The premature group corrected for gestational age did not differ significantly from the control group. Strabismic children have a delayed maturation for the

second-order process only. Our psychophysical investigation has underlined differences in first-order and second-order motion systems implying the existence of two different mechanisms. The development of premature children (without pathology) is similar to the normal development. Results of the strabismic group confirm a disorder in complex motion perception.

◆ **Modal and amodal contour completion in infancy**

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Visual system often interpolates missing structures in the stimuli. This ability is called visual completion which can be modal or amodal. On the basis of a psychophysical study on adults, Kellman et al (1998 *Journal of Experimental Psychology: Human Perception and Performance* **24** 859–869) argued that a common mechanism underlies modal and amodal completion: the 'identity hypothesis'. However, some other studies cast doubt on this hypothesis (eg Anderson et al, 2002 *Cognitive Psychology* **44** 148–190). We examined the development of these two kinds of visual completion in infants aged 3 to 8 months. The infants were familiarised with a display composed of a partially overlapping circle and square. After familiarisation, the infants were tested on the discrimination between a complete figure and an incomplete figure. If infants could perceptually complete the figures in familiarisation display, they were expected to show novelty preference for the incomplete figure. There were two kinds of familiarisation displays: (i) the colour of two figures was the same, and (ii) the colour of two figures was different. The former was a spontaneously splitting display, which produced alternately illusory contours of a partial circle and a square. The latter was an occlusion display, which could produce amodal completion of the overlapping region. For each display, tests were carried out on three age groups (3–4, 5–6, 7–8 months) of eight infants. Our results suggest that completion of modal contours develops earlier than that of amodal ones.

◆ **Language and categorical perception of colour: Developmental and cross-cultural approaches**

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After familiarisation to one hue, infants at 4 months show novelty preference to stimuli that cross a category boundary but not to stimuli from within the same category. This categorical perception (CP) occurs across blue–green and blue–purple boundaries (Franklin and Davies, submitted). Here, using the same stimuli (cross-category and within-category stimulus pairs equated in Munsell hue steps), we investigated the effect of colour naming on CP. In experiment 1, using a 2AFC task modified for use with young children, we assessed CP in forty children aged 2 and 3 years. CP was shown for both boundaries, with higher accuracy for cross-category rather than within-category choices. However, CP was independent of correct naming. In experiment 2, CP was assessed in one hundred and six English and Ovakwanyama children aged 4–8 years. Ovakwanyama—a Namibian language—has one basic colour term (BCT) that includes blue and green and has no BCT for purple. CP was assessed by using a visual-search task with cross-category and within-category target–distractor arrays. Children were faster at locating targets on cross-category arrays, but Ovakwanyama children showed no categorical effect across the blue–green boundary. Individual patterns of naming had no effect on CP. Both experiments are discussed in relation to the impact of language on CP.

◆ **Comparison of visual illusions in children and adults**

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The term 'visual illusion' embraces a wide range of phenomena: systematic biases in the perception of size and colour, incorrect interpretation of stimulus–surround relationship, generation of phantom images, etc. It is evident that different phenomena from this list could originate from errors and limitations of information processing at different levels and in different parallel pathways of the human visual system. Since many components of this system develop gradually and mature at different rate, one would presume that different visual illusions would demonstrate different dependence on subject age. We confirmed this conjecture by comparing the quantitative estimates of fifteen classical illusions (reported by Müller-Lyer, Hering, Necker, Kanizsa, and others) in children and adults. To measure the illusions, we used some modifications of the standard test stimuli which did allow us to judge not only the presence of each illusion but also its strength. More than two hundred children aged 6–7 years and two hundred young adults were examined. Diploma students N Gagarina and N Talianskaya took part in gathering the data. It was found that certain illusions were almost equally strong in children and adults (eg the Müller-Lyer

illusion), while others were much more pronounced either in children (eg illusions based on the perspective cues) or in adults (eg overestimation of the vertical lines, appearance of Kanizsa figures). In the cases of all illusions, scatter of the data was higher in children than in adults, although, in special control experiments on length estimation, the reverse applied. Our results indicate that assessment and comparison of visual illusions in subjects of various ages could help to trace the developmental changes of certain visual mechanisms.

◆ **The perception of subjective contours in youth and old age**

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A Piagetian paradigm was used to assess perceptual development in a pre-operational group ($n = 16$, age = 5 and 6 years), and a concrete operational group ($n = 16$, age = 7 and 8 years) with subjective contour (SC) displays. All subjects were naïve regarding the perception of SCs. Each participant was tested individually on four different SC displays for both latency of verbal identification (perception) and reaction time for matching the subjective to real contours (recognition). The perception condition revealed highly significant differences of age, type of SC, and an age \times SC interaction between the two groups. In the recognition condition only the age factor yielded significance. These findings support an interpretation that different stages of development use different perceptual responses to SCs. In a second study, we examined whether an elderly population ($n = 20$, age = 62–92 years) would respond to SC stimuli differently than a younger age group ($n = 20$, age = 20–28 years), with both groups naïve to SCs. Tested on 4 SC stimuli, the older group had a highly significant mean recognition time, suggesting that the perception of SCs decreases with age and also implying that cognitive mechanisms are involved in their perception.

◆ **Visual localisation of the centre of triangle shapes in young children and adults**

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The ambiguity of the notion of centre for most shapes raises the question whether children perceive the centre of a shape in the same place as adults (Baud-Bovy and Soechting, 2001 *Journal of Experimental Psychology: Human Perception and Performance* **27** 692–706). To answer this question we asked five-year-old children and adults to mark the centre of a triangle with a pen. The responses of children and adults were strikingly similar. First, the two groups perceived the centre of right triangles at mid-distance between the centre of mass and the centre of the inscribed circles. Second, the perceptual centre of the equilateral triangle was shifted toward the vertex that opposed the horizontal edge of the triangle for children and adults alike. These results indicate that the processes involved in this task are in place since at least the age of five and do not depend on any sort of explicit training with geometric figures acquired later in school. These results are in line with a 'continuum' model of the development of knowledge [Melher and Bonati, 1998 *Developmental Cognitive Science* (Cambridge, MA: MIT Press); Spelke, 1998 *Infant Behavior and Development* **21** 181–200].

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◆ **Older adults derive neither more nor less benefit from word context than do younger adults in a crowding task**

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For younger adults, the middle letter of a three-letter sequence is identified more accurately when it is part of a word than when it is part of a non-word (Fine, 2001 *Optometry and Vision Science* **78** 831–838). Word context appears to reduce the impact of visual crowding. Older adults are more susceptible to visual crowding than are younger adults (Fine, 2002 *Perception* **31** Supplement, 169). Here, I investigated whether word context reduces the impact of crowding to a similar extent in older adults. Seven younger (23-year-old) and seven older (65-year-old) volunteers with normal visual acuity participated. Each identified letters presented alone and letters flanked by one letter on each side forming either trigrams or three-letter words. For the younger group, stimuli were presented for 50 and 100 ms; for the older group, stimuli were presented for 100 and 200 ms. There was a significant group \times stimulus type \times duration (fast and slow) interaction ($F_{2,24} = 9.6$, $p < 0.002$). The results for the younger group did not depend on duration; the older

group performed significantly better on the trigrams and words with the 200 ms duration. The 100 ms data for both groups showed a significant effect of group ($F_{1,12} = 7.4$, $p = 0.019$) and stimulus type ($F_{2,24} = 243.1$, $p < 0.001$), but no interaction between these variables ($F_{2,24} = 1.7$, $p = 0.208$). As in previous experiments, older adults were more susceptible to visual crowding. However, they derive neither more nor less benefit from word context than do younger adults.

◆ **Personal identity and handwriting discrimination: A developmental study**

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Observers are sensitive to small distortions of handwritten words. A normal word and a 12% horizontally stretched word are correctly discriminated by most children and adults. However, discrimination performance is affected by stimulus inversion, writer's identity, and observer's age in a complex way. Three groups of participants (8-year-old children, 10-year-old children, young adults) were compared. The experimenter required participants to copy a set of printed words using their own handwriting. One week later, participants were asked to discriminate words written by themselves and, in a different block, by the experimenter. Every trial included a normal word and a distorted word, in either upright or inverted orientations. Sensitivity to the geometrical distortion was better in the inverted orientation; which is consistent with the general hypothesis that meaningfulness interferes with low-level discrimination. More interestingly, the superiority for inverted words was larger for the non-personal handwriting only in children; in adults, the inversion effect was equally strong for personally and non-personally handwritten words. Children are marginally affected by inversion of their own handwriting, but strongly affected by inversion of the unfamiliar handwriting. In adults, the sensitivity to geometrical distortions of handwriting is unaffected by writer's identity.

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◆ **Local processes and long-range effects in the identification and discrimination of visual patterns**

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We present results from identification and discrimination experiments with complex stimulus patterns (superpositions of Gabor and weighted Hermite polynomial patches), shown either with or without surrounding patterns (Gabor patches). The data support the following hypotheses: (i) Patterns are identified not only with respect to components relevant for a correct identification or discrimination, but with respect to the complete stimulus pattern; the finding is not compatible eg with the notion of probability summation, but, is instead, with that of template formation according to some form of Hebb's rule. (ii) Although subjects were instructed to focus on the stimulus pattern, the surrounding patterns influence the subjects' responses via long-range connections modulating the sensory representation of the stimulus patterns: surrounds defined by low-spatial-frequency components imply an increase of confusions with stimuli defined by lower spatial frequencies, and high-frequency surrounds imply an increased number of confusions with patterns defined by higher-spatial-frequency components, where the strength of these effects depends upon the distance of the surround patterns from the fixation point. The data suggest that the concept of local Hebbian adaptation has to be generalised such as to account for the observed surround effects, possibly along the lines of the model of Adini et al (2002 *Nature* **415** 790–793), assuming Hebbian and anti-Hebbian synaptic learning; alternatively, they may be discussed without reference to Hebbian adaptation, eg in terms of the models of Somers et al (1998 *Cerebral Cortex* **8** 204–217) and Deneve et al (1999 *Nature Neuroscience* **2** 740–745).

◆ **Learning spillover to invisible dots**

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Does subliminal learning occur only as a result of passive processing of a visual stimulus? To address this question, we presented subjects with four different directions of low-coherence moving dots, such that the direction of coherence was below the perceptual threshold. Each direction of motion was presented for an equal number of trials; however, one direction was paired with targets of a letter-identification task. The visibility of the moving dots was varied in two distinct ways in a series of experiments. In the first series of experiments, we manipulated

the coherence of the dots' movement. The results revealed that learning occurs from unperceived 'invisible' motion. In the second series of experiments, we varied the contrast of the dots. In these experiments we showed that invisible dots (below the contrast detection threshold) also elicit learning. If learning is passive, thresholds should improve equally for all the presented directions. On the other hand, if learning is formed only on a feature to which attention is directed, no improvement should be found for any presented direction. Contrary to these hypotheses, the threshold improved for the paired direction, but not for the other directions. While these results are at odds with the passive-learning hypothesis as well as the focused-attention hypothesis, they are consistent with classical conditioning, in which arbitrary features are learned when paired with rewarding or noxious stimuli.

◆ **Invariant recognition of visual images in monkeys: Dependence on visual attributes**

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To understand a possible mechanism of invariant visual recognition in rhesus monkeys, we have studied the characteristics of learning processes involving visual discrimination of stimuli with different visual attributes (geometrical figures of various shape, size, orientation; various spatial relationships between components of objects). After complete training to visual discrimination, the monkeys were tested for invariant recognition of the same stimuli, after their transformations such as variation in size, shape, and spatial relationships. Monkeys' correct decisions, refusals of task decision, and motor reaction time were recorded. An analysis of monkeys' behaviour characteristics revealed significant differences caused by visual attributes. When monkeys were required to discriminate black-and-white geometrical figures of different shape or orientation under a transformation such as some variation in shape of some objects, this transformation practically did not influence correct decisions. If monkeys performed the discrimination of geometrical figures of different size, or of complicated images with different spatial component relationships under variation in these spatial characteristics, the correct decisions significantly decreased. These changes are accompanied by a corresponding significant increase of refusals of task decision and of motor reaction time. The invariance of this discrimination is achieved by some training. The results obtained suggest that the basis for invariant recognition of the visual images is the existence in the visual system of separate channels for processing information concerning the shape of an object and its spatial characteristics (size and component relationships). The level of decision-making is included to form common visual image.

◆ **Eye movements to multi-shape scenes and statistical learning of shape conjunctions**

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We explored the extent to which automatic learning of co-occurrence statistics of shapes by passive viewing of multi-shape scenes was correlated with the eye movements made during inspection of the displays. Shapes were grouped into six 2-element base-pairs, each with a specific spatial arrangement. During the practice phase, subjects viewed displays composed of a random arrangement of three base-pairs while their eye movements were monitored. During the test phase, subjects viewed one base-pair and one arbitrary pair, in a temporal 2AFC task and were asked to choose the more familiar pair based on the practice phase. Subjects selected the base-pairs significantly more often (64% correct, $p < 0.001$). Individual subjects who performed above average made 10% more saccades in the last than in the first quarter of the practice phase ($p < 0.005$), and spent 9% less time overall ($p < 0.001$) and 10% less time per fixation ($p < 0.05$). However, the proportion of saccades between two elements of the same base-pair compared to saccades between different base-pairs did not change with practice ($p > 0.8$). Thus, when subjects implicitly learn higher-order spatial statistics, the overall efficiency of their gaze improves, but learning does not occur by the eyes tracking the significant spatial structures in the scene.

◆ **Neural specialization for letter processing under different learning conditions**

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Functional MRI can reveal neural specialization. Polk et al (2002 *Journal of Cognitive Neuroscience* 14 145–159) found that a 'letter area' in the left fusiform gyrus (LFG) responds more to familiar English letters than to either digits or shapes. Other studies show that silent reading of text, letters, activates Wernicke's area, which is involved in language. Pelli et al (2003 *Vision Research* 43 in press) showed that, after only a few thousand trials, observers attain the proficiency of native readers in identifying letters of a foreign alphabet, but fail to improve their

initial meagre memory span for the foreign letters. More extensive learning is required to increase the memory span. Is the neural activity in these two areas (LFG and Wernicke's) correlated with the quickly learned letter identification, or with the slowly attained large memory span characteristic of fluent readers? We used fMRI to measure neural activity while observers identified letters of both the English and Hindi alphabets. We tested readers of English only and bilingual readers of English and Hindi. For bilingual readers, the LFG and Wernicke's area were similarly activated by both alphabets. Before training, for English-only readers, the LFG was more activated by English letters, and Wernicke's area was activated only by English letters. After two thousand trials of training, LFG activation by Hindi letters increased to match that of English letters, while activation in Wernicke's area did not change. Our results show two kinds of letter specialization, one in the LFG correlated with quickly learned letter identification, and another in Wernicke's area associated with slowly expanded memory span and linguistic learning.

◆ **Is colour bound to spatial location in long-term picture recognition memory?**

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We investigated the roles of colour and spatial location in long-term picture recognition memory, using stimuli (240 photos of room interiors) that were categorically homogeneous and difficult to verbalise. In the learning phase, subjects were shown 60 colour photos and 60 gray-scale photos for 5 s each. After a 30-min break, subjects were tested with 120 old photos and 120 new photos presented one at a time. In experiment 1, we examined whether representations of colour in memory are tied to representations of spatial location. In order to dissociate colour from spatial location without disturbing shape or spatial relationship, we left-right (L-R) reversed half the old colour and old gray-scale photos in the testing phase. Ten male and ten female subjects participated. Regardless of the sex of subjects, reversal had no effect on recognition of gray-scale photos, suggesting that representations of gray-scale shape are only weakly bound to spatial location. In females, L-R reversal had no effect on recognition of colour photos. Females recognised colour photos better than gray-scale photos regardless of whether they were L-R reversed or not ($p < 0.01$). In males, L-R reversal significantly lowered recognition of colour photos ($p < 0.01$). Male recognition of L-R reversed colour photos was no better than recognition of unaltered or reversed gray-scale photos. Using ten male and ten female new subjects, experiment 2 replicated experiment 1 and also showed that this sex difference was not due to differences in intentional memory strategies. These results suggest that, in males, colour is bound to spatial location in picture memory. Recognition of scenes by females, on the other hand, may rely on representations of colours and/or objects that are more spatially independent.

◆ **Influence of characteristic object colour on colour naming**

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Characteristic colours that are recalled in association with familiar objects in long-term memory are called memory colours. We examined the influence of memory colours on colour perception by means of a colour-naming task. In the experiment, we showed coloured images on a computer monitor. Subjects had to assign each image to one of eight basic colour categories (yellow, orange, red, violet, blue, turquoise, green, grey). The images showed photographs of different common known kinds of fruits (eg banana, lettuce, etc) on a neutral grey background. Each photograph showed a single fruit object. In further conditions, we showed the same images with all the pixels randomly interchanged, uniformly coloured contours of the fruit objects, circular cut-outs taken from the fruit object, or circular patches of uniform colour. For each image, the average colour within the fruit object or circular patch could be set to an arbitrary value. For example, the banana could be displayed with a space-averaged colour of yellow, blue, or grey. For each condition, 225 colour variations of each image were presented in random order for 500 ms. These images were distributed regularly across the available colour gamut at a constant luminance. The results for photographs of fruits show that the category of the characteristic colour of the perceived object is massively enlarged compared to categorisation of the corresponding fruit-outline patches and circular cut-outs. Compared to neutral patches, the characteristic colour category was enlarged for fruit contours as well. In our experiments we could show a strong influence of memory colour on colour perception.

◆ **Short-term visual memory conserves chromatic contents per se under luminance distraction**

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To clarify how colour perception is memorised, we investigated whether chromatic signal being produced in early visual systems is tied to short-term memory with or without any modification. We measured the effects of 2-D dynamic luminance noise on chromatic discrimination thresholds at a delay of 900 ms after visual stimulation. Subjects were asked whether colour of a reference patch was the same as that of a test patch. All stimuli were displayed on an RGB monitor. In a sequence of stimuli, 250 ms masking noise was presented successively between a reference (250 ms) and a test patch (250 ms). A blank period (200 ms) separated the reference, the noise, and the test. Patches and noise were of 2 deg × 2 deg square and were surrounded by 21 deg × 16 deg background. Each subject set the equiluminance of all tests and the background. We varied the contrast of luminance noise. In a control experiment, we measured chromatic discrimination thresholds with the use of a bipartite stimulus in the absence of a luminance masking noise. Thresholds of chromatic discrimination were found to be constant with increasing contrast of the noise. The chromatic discrimination thresholds in short-term visual memory are not greatly different from those in a bipartite experiment. In human short-term visual memory mechanisms, chromatic signal is retained at least up to an early visual storage, indicating that colour sensation is registered for a second, even if achromatic signals enter the early storage of human memory systems.

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◆ **Objects and inter-object relations in visual working memory**

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Recent studies (Luck and Vogel, 1997 *Nature* **390** 279–281; Vogel et al, 2001 *Journal of Experimental Psychology: Human Perception and Performance* **27** 92–114) have indicated that visual working memory stores integrated objects rather than individual features such as colour, orientation, and shape. The nature of these visual objects and the storage mechanisms of their features in working memory remain conflictual issues in the literature (Wheeler et al, 2002 *Journal of Experimental Psychology: General* **131** 48–64). Are the features of visual objects stored only individually in something like a list or 'object file'? Or is there another form of object-identity information which concerns inter-object relations that determines posterior recognition, and that derives from the objects being part of the same scene? In our study, we used a change-detection paradigm to investigate how features of different objects are tied to each other. We studied how the performance in object feature identification depended on whether the features of non-target objects in the scene remained the same or not. The preliminary results on colour showed that there is an effect of non-target change on target identification. These results are extended to feature dimensions of orientation and shape. We also show how the presence of changing distractors interferes with target object feature identification. The results support the idea that visual objects in working memory are not just lists of feature information (conjunctions) but that there is a relational form of object-to-object information that is involved in visual working memory.

◆ **Competition in visual working memory for control of search**

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Recent perspectives on selective attention posit a central role for visual working memory (VWM) in top-down control of attention. According to the biased-competition model (Desimone and Duncan, 1995 *Annual Review of Neuroscience* **18** 193–222), active maintenance of an object in VWM gives matching (Downing, 2000 *Psychological Science* **11** 467–473) or related (Moore et al, 2003 *Nature Neuroscience* **6** 182–189) objects in the environment a competitive advantage over other objects in gaining access to limited processing resources. Participants in this study performed a visual-search task while simultaneously maintaining a second item in VWM (cf Woodman et al, 2001 *Psychological Science* **12** 219–224). On half of the trials, this item appeared as a distractor item in the search array. In three experiments we found no evidence that this item interferes with successful attentional selection of the search target. In contrast, we found some evidence to suggest interaction between items in VWM at the level of response selection. These results are consistent with two types of model, one in which a neural representation of

the current task biases the competition between items in a unitary VWM (eg Wallis et al, 2001 *Nature* **411** 953–956), or one in which VWM is fractionated to allow for maintenance of critical items that are not immediately relevant to the task (eg Oberauer, 2002 *Journal of Experimental Psychology: Learning, Memory, and Cognition* **28** 411–421).

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◆ **Multi-item working memory in macaque monkeys**

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We investigated primate performance in a behavioural task that requires holding several visual images simultaneously in working memory. Two macaque monkeys were trained on a delayed-match-to-sample task with multiple samples. In each trial, a sequence of 1–7 different images served as samples. These were followed by a match stimulus, which was a repetition of one of the samples (the cue). The length of the sequence and the position of the cue in the sequence were chosen at random on each trial. The monkey's task was to recognise the appearance of a repetition of any one of the samples and therefore the monkey needed to hold in working memory all the images of the sequence. Two type of errors occurred. One was 'misses'—a failure to detect the repetition. We found that the distribution of these errors depended on the position of the cue in the sample sequence: The greater the cue–match separation, the poorer the performance. Surprisingly, for fixed cue–match separation, performance improved with increasing sequence length, ie with the number of items in working memory. The other error was 'false positives'—a response erroneously reporting repetition, following a sample stimulus presented for the first time in the current trial. Distribution of these errors increased with the time and number of stimuli since the beginning of the trial. Our findings are consistent with a model (Amit et al, 2003 *Cerebral Cortex* **13** 435–443) suggesting that noise, associated with neural dynamics, spontaneously erases items from working memory (leading to misses) and induces 'ghost' memories of familiar, unseen stimuli (leading to false positive errors).

◆ **The effect of imagery on mental rotation: An ERP study**

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Study of the processes contributing to visual imagery or 'seeing with the mind's eye' continues to be of major interest in cognitive psychology. One interesting issue is the analysis of the hypothetical component processes contributing to mental rotation and imagery. We therefore attempted to examine the processes related to storage in visual short-term memory and mental transformation by separating them in time in a modified parity-judgment task using event-related brain potentials (ERPs). In the perceptual condition, participants were asked to determine whether two successively presented letters (S1–S2 interval of 2500 ms) were identical or different, irrespective of their orientation. In the imagery condition, subjects were asked to imagine the first letter stimulus (S1), then to rotate it by an angle indicated by an arrow cue, and finally to compare this image with S2. Simultaneously, multi-channel ERPs were recorded that revealed brain activity in different brain regions with millisecond resolution. Behavioural differences between perception versus imagery condition were revealed by a linear RT increase with angular disparity from the upright in the perception but not in the imagery condition. In addition, only in the imagery conditions was performance improved when both S1 and S2 matched rather than not. The analysis of ERPs showed that lateral extrastriate brain regions were more strongly activated in the imagery condition during the S1–S2 interval. In addition, we found also evidence for the contribution of motor-related brain regions during imagery. In conclusion, present results argue for a partial overlap of perception-related and imagery-related brain processes.

◆ **Priming of pop-out—an fMRI study**

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In visual search, each trial sets up a memorial trace that affects the search performance in the following three to twelve trials. This has been called 'priming of pop-out' or 'repetition effect in visual search'. We executed a rapid-presentation event-related fMRI study and examined the neural basis of this effect. Observers were simply required to respond to the subtle shape of the odd-coloured target in a display. The target colour and position switched randomly from trial to trial. With respect to the target colour or position, the trial sequences that contained several repetitions and repetition violations were identified for analysis. Comparison between the repeated and violated

trial sequences revealed that bilateral posterior parietal areas and middle frontal gyri were more involved in both colour-repetition and position-repetition violation. Anterior cingulate was additionally involved in the position-repetition violation. Bilateral visual cortices, posterior part of the cingulated gyrus, and right temporoparietal junction showed more activation in the position repetition than in its violation, and superior part of the bilateral precentral gyri showed more activation in the colour repetition. These results support the view that priming of pop-out recruits relatively primitive cortical circuit in addition to the frontoparietal network. In the above cortical areas, bilateral posterior parietal areas, middle frontal gyri, and anterior cingulate showed parametric increase of the BOLD signal change as the number of the repetition before the violation increased. Other areas did not show such a modulation, suggesting that these areas were involved in the task process itself.

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CROSS-MODAL INTERACTIONS

◆ Localisation and form recognition in sensory substitution

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Sensory-substitution systems allow blind people to 'see' via tactile or auditory stimulation. The sensorimotor contingency approach can explain this possibility of having a visual experience via channels other than vision by the following idea: What is perceived and recognised is not passively received sensory input, but is constituted by the laws linking subject's actions to the sensory changes that result from them. We followed this theory in order to understand how users can reach the mastery of sensory substitution devices. More precisely, we attempted to determine the different stages involved in the mastery of a particular visuo-auditory device: The vOICE developed by Peter Meijer. We have named these five stages: contact, exteriorisation, spatialisation, comprehension of the information, and immersion. We attempted to understand how, in advancing through these different stages, subjects pass from a kind of deductive reasoning to a form of immediate apprehension of what is perceived. We especially tested the ability of localisation of objects and the ability of form recognition and categorisation of these different forms. These experiments were done with six sighted subjects who were blindfolded. On average, the experiments took between 10 and 15 h.

◆ Visual – auditory localisation performance: Is the whole better than the sum of the parts?

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In the everyday life, synergetic sensory information is integrated by the central nervous system in order to provide a reliable perception of the environment. Visual – auditory localisation is of specific interest in the investigation of multisensory integration since the visual and auditory systems provide different cues for spatial processing: retinotopic for vision, tonotopic for audition. Such characteristics support the evidence that the visual system is more appropriate to spatial analysis than the auditory system. Furthermore, auditory spatial resolution is worse in the vertical than in the horizontal direction. Therefore it is assumed that the relative weight of each modal component for perception varies depending on bimodal target location in azimuth and in elevation. We investigated localisation performance in the two dimensions of space from behavioural data collected with a psychophysical paradigm. Visual, auditory, and visual – auditory responses were analysed through their distribution characteristics, such as the centre of gravity, orientation, and variation in the orthogonal directions. By translating the notion of ecological advantage gained from integration into a quantitative measure, it is possible to formulate a computational model of visual – auditory integration in a localisation task. The modeling of the data was found to support the maximum-likelihood-estimation (MLE) model, although it appears to fit differentially according to the position of the stimulation in space (combination of azimuth and elevation). The results are in line with integrative processing applying in the visual – auditory localisation task, with a variable weight of each modal component following the rules of auditory spatial processing.

◆ **Can attention to one of two competing visual stimuli bias auditory aftereffects?**

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The strength of the loudness-change aftereffect (LAE) following auditory adaptation is affected by the presence of a congruent visual stimulus during adaptation; in fact, adapting to a visual stimulus alone produces an LAE. In contrast, congruent auditory stimuli fail to affect the strength of visual aftereffects (VAE) (Kitagawa and Ichihara, 2002 *Nature* **416** 172–174); this may explain why Rees et al (2001 *Neuropsychologia* **39** 937–949) failed to obtain influences of attending to auditory stimuli on VAE. We studied whether visual attention can bias the LAE. Seven subjects adapted to a purely visual stimulus: an expanding disk of colour 1 (E1) and a contracting disk of colour 2 (C2) for 2 s, to the right and left of fixation, respectively; the locations of the disks E1 and C2 were exchanged for the next 2 s. This was repeated 30 times, for an initial adaptation of 120 s. The two colours were red and green. Within a session, subjects attended selectively to one type of disk, ignoring the other type. They were tested with a brief fixed-loudness tone after adaptation; the 2AFC task was to report whether they perceived the tone as increasing or decreasing in loudness. Each of the nineteen subsequent re-adaptations lasted for 12 s. The type of the attended disk and combinations of disk colours and size changes (E1–C2 and E2–C1) were balanced randomly across sessions. In general, attending to the contracting/expanding disk tended to produce an increasing/decreasing LAE. Differences in the percentage of increasing-loudness responses after attending to contracting and expanding disks averaged 8.75 percentage points. Selective attention to one of two competing visual stimuli may produce an LAE. These findings provide evidence for possible inter-modality attentional influences.

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◆ **Useful attributes of visual and auditory information for emotional expressions**

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We investigated to which degree and at what timing visual information and vocal information contribute to emotional categorisation and what acoustic attributes are critical for emotional definition. Two kinds of short sentences with neutral content were emotionally spoken by using vocal intonation (auditory information, A) and facial expressions in movements (visual information, V). The emotional expressions produced by a professional actress were one of the following six kinds: happiness, surprise, sadness, fear, disgust, anger, plus a neutral one. The stimulus duration t was divided into four periods: t_1 —the duration from the start to a quarter of the full period, t_2 —duration from the start to half of the full period, t_3 —the duration from the start to three-quarters of the full period, and t_4 —the full duration. Ten participants observed and categorised the stimulus presented in one of the three modes, only V, only A, or V + A under one of the four time conditions. We found that expressions to which visual and vocal information almost equally contribute were happiness, sadness, and the neutral expression. Visual information was more effective in expressing disgust and fear, while surprise and anger were well identified with vocal information. Visual information started first and continued to the end of the stimulus, but vocal information was heard only during t_2 and t_3 , with only surprise mostly identified during t_1 . Acoustic analysis was done for each emotion.

◆ **Auditory 'capture' of visual motion**

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Visual perception is significantly altered by auditory stimuli. We asked whether the perceived direction of visual motion could be influenced by auditory signals. The visual stimulus was a spatiotemporally vignetted sine-wave grating. Multiple 'frames' of this stimulus were combined into short movies. Each frame lasted 125 ms, and each movie consisted of 3 frames. Between successive frames, the spatial phase of the grating was altered. Nine phases were sampled, ranging from 90° to 270° in increments of 18°. An interframe phase shift of 180° produced a movie in which the direction of grating drift was ambiguous and bistable. Interframe phase shifts of 90° or 270° produced unambiguous apparent motion. We paired the presentation of the movies with auditory stimuli. The auditory stimulus was a binaural amplitude-gated burst of pink noise. In the rightward sound condition, the sound-source onset at a point 2 virtual metres to the left of the subject's head and moved at a constant velocity to a location 2 virtual metres to the right of the head. The opposite occurred in the leftward sound condition. There was also a

no-sound control condition. Observers ignored the auditory stimulus and judged the direction of visual motion. The perceived direction of visual motion was strongly influenced by the direction of concurrent auditory motion. Auditory motion not only 'captured' ambiguous visual motion, but could even reverse the perceived direction of unambiguous visual motion. These results suggest that visual motion, a dynamic and spatiotemporal aspect of visual perception, can be altered by sound. Additional experiments exploring whether the influence of auditory motion on visual motion extends to the facilitation of motion discrimination thresholds are presented.

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◆ **Catching audio-visual mice: The extrapolation of audio-visual speed**

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We investigated how humans combine information from the auditory and visual modality in an active perception task. We found that the precision for predicting the location of a moving object was improved when speed signals were provided in both modalities. The observer was seated in front of a 180° arc containing 35 equidistant LEDs and loudspeakers. To simulate a running audio-visual mouse, the LEDs and loudspeakers were switched on and off such that object movement from left to right or vice versa was generated. The task of the observer was to predict the arrival time of the mouse in the centre of the arc by pressing a button. We measured the accuracy of the estimated arrival time for the auditory, visual, and bimodal conditions at five different speed levels, and compared it with model predictions. We measured the mean and variance of the estimated arrival time and found a significant, signal-duration-dependent bias of the estimated arrival time and an increased response variability for slower motion speeds. The means for the different modality conditions did not differ significantly from each other within single speed levels. The variability of the bimodal estimates, however, was significantly smaller than for unimodal signals at all motion speeds. The model predictions are based on the assumption that human observers combine the auditory and the visual senses such that the variability in the bimodal condition is minimised (maximum-likelihood integrator). The mean predicted arrival time matches the observed bimodal data, but the predicted variability is about 10% smaller than the observed variability at all motion speeds. We conclude that human observers are slightly sub-optimal in combining co-localised auditory and visual signals in a speed-prediction task.

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◆ **Auditory resolution and flash-lag effect**

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When a brief flash is presented aligned to a moving stimulus, the flash is perceived to lag behind the moving target (the flash-lag effect, or FLE). Recently we have shown that the FLE is not limited to vision, but also occurs in audition, and cross-modally (Alais and Burr, 2003 *Current Biology* 13 1–5). Here we study further the cross-modal FLE and search for differential latencies that may explain it. Using a technique devised by Murakami, we displayed stimuli—either visual Gaussian blobs or acoustic noise bursts—randomly in one of three possible positions. On the appearance of a brief 'flash' (again either visual or acoustic), subjects were required to report the apparent position of the randomly moving stimulus: a tendency to report the hopping stimulus in its next rather than actual position indicates flash-lag. We found strong flash-lag for conditions of visual motion and acoustic flash: the other conditions were near veridical, suggesting small or zero flash-lag effects. To test whether the cross-modal FLE could be explained by different neural latencies for the different modalities, we measured separately visual and auditory latencies with two techniques: temporal adjustment and reaction times. With both methods, a brief static acoustic stimulus was perceived more rapidly than a brief static visual stimulus. However, the perception of a sound source in motion was slow compared with a comparable visual stimulus. These findings cast doubts on many of the standard explanations for the flash-lag effect, including motion interpolation, differential latencies, and temporal integration.

◆ **Cross-modal interaction: Visualisation of pseudo-words**

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According to Köhler, some phonetic patterns can be associated with visual patterns, eg takete can be taken as a pseudo-name for sharp, angular patterns, and maluma as a pseudo-name for smooth, curvilinear patterns [Köhler, 1949 *Gestalt Psychology* (New York: Liveright)]. Our previous studies have shown that particular sets of phonemes and consonant–vowel patterns have a higher probability of production in pseudo-names for abstract visual patterns with particular physical characteristics (Janković and Marković, 2001 *Perception* 30 Supplement, 29). In the present study two groups of prototype pseudo-words were constructed with appropriate phonetic and consonant–vowel pattern structures. In phase I, subjects were asked to produce monochromatic abstract visual patterns corresponding to presented pseudo-words. In phase II, another group of subjects was asked to (a) judge physical features of extracted visual patterns on bipolar seven-step scales (lightness–darkness, compactness–dispersion, simplicity–complexity, etc), and (b) give subjective judgments of patterns on visual semantic differential scales (scales converged into following factors: evaluation, interestingness, regularity, potency, and activity). The results showed that the most discriminative feature is sharpness, followed by complexity, lightness, compactness, etc. Cluster analysis and multidimensional scaling on physical similarity data showed that extracted visual patterns can be clearly categorised in two clusters that correspond with two clusters of pseudo-words.

◆ **Touch can influence visual depth reversal of the Necker cube**

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Three-dimensional (3-D) information about the shape of an object can be obtained by touch as well as vision. We investigated whether haptic information contributes to 3-D interpretation of ambiguous visual patterns. The Necker cube is a well-known example of ambiguous visual patterns, which causes spontaneous alternations of bistable 3-D percepts. To measure the amount of haptic influence on the perception of the Necker cube, a force-feedback device was used to generate a virtual haptic cube, which is consistent with either of the two visual interpretations. The subjects' task was to report, by pressing a key, which 3-D shape was perceived when they were touching the virtual haptic cube along a pre-defined trajectory on the cubic surface. To examine haptic influence on the bistable percepts, the duration of each percept was recorded. The subjects also performed a control task that required eye movement along the trajectory without any haptic feedback. We found that the duration of the visual percept consistent with the haptic information was much longer than that in the inconsistent case. This duration difference is not explained by visual attention, since the results of the control task showed that the eye movement alone did not have as much effect. We therefore consider that haptic information of the surface shape influences visual depth reversal of the Necker cube. The results suggest that haptic signals can impose a dynamic constraint on visual computation of 3-D shapes. [Supported in part by the Telecommunications Advancement Organization of Japan.]

◆ **Latencies of saccadic eye movements during reaching and grasping when target position is suddenly changed**

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Using a virtual-reality technique, a double-step experiment was undertaken to investigate the performance of reaching and grasping. In the experiment, subjects reach and grasp target object images that appear in the stereo graphics display. During reaching, the target suddenly changes its position when the subject's hand comes within a certain distance D from the starting position. Subjects tended to grasp the initial target position and then re-grasp the second position in the case of large D conditions. Analysis of the velocity profile of the reaching movement revealed that a certain duration between the velocity peak and the end of the reaching motion is necessary to avoid grasping the initial position. In the present research, saccadic eye movements were measured simultaneously in the same double-step experiments. Five undergraduate students participated as subjects. For every subject, a saccade to the second target position occurred 200–500 ms after the target position changed, followed by correction of the movement. The latency of saccade was measured for the following conditions: (i) $D = 1$ cm, (ii) $D = 20$ cm, and (iii) without reaching. In condition (i), the target position changed before the peak velocity of reaching and most of the subjects were able to change the movement and grasp the second target

position. In condition (ii), re-grasping was observed in all subjects. The average latencies were (i) 243 (SD 39) ms, (ii) 319 (SD 79) ms, and (iii) 291 (SD 38) ms. These results show that gaze can be easily altered at the beginning of reaching movements, but tends to be fixed to the target after the peak velocity. We conclude that the state of visual attention differs, depending on the stage of motor activity (reaching/grasping).

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◆ **Cross-modal attentional interference in rapid serial visual-and-tactile presentations**

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The phenomenon that the processing of the first target interferes with that of the second target in rapid serial visual presentations (RSVPs) is referred to as an attentional blink (AB). We studied the attentional interference between visual and tactile processing in line with AB researches. The alphabetic letters in black were presented in RSVPs, and vibro-tactile stimuli were presented by the vibrator simultaneously with a letter in rapid serial tactile presentations (RSTPs). The SOA was 80 ms and the presentation duration was 40 ms for both visual and tactile stimuli. In the experimental condition, the subjects were required to conduct two kinds of tasks. The first task was to detect a white letter (the first target) embedded in black ones, and the second task, so called probe task, was to report whether or not a tactile stimulus (the second target) with a longer duration (65 ms) than the other tactile stimuli was embedded after the first target. The second target was presented on 60% of trials. In the control condition, the subjects were asked to ignore the first target and conduct only the second task. We found that the detection accuracy of the second target was reduced for about 240 ms after the first target was displayed. That is, we established the existence of a visual-tactile attentional blink. In addition, the accuracy of the control condition was lower than in the previous AB studies. These results suggest that visual processing interferes with tactile processing automatically in cross-modal (ie visual and tactile) rapid serial presentations. We discuss these results in terms of the cross-modal processing and the limited capacity account of the AB.

◆ **Visual perception of the gravitational orientation: A study of the role of angular size of the stimulus, gender, and countertorsion of the eyes**

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In darkness, head tilts are known to induce constant errors in the perception of the vertical. Adjustments are displaced either in the direction of the postural inclination (A effect) or in the opposite direction (E effect). These effects depend on both the magnitude of tilt and the perceptual modality in which the rod adjustments are made (Luyat and Gentaz, 2002 *Journal of Experimental Psychology: Human Perception and Performance* **28** 1002–1011). The contribution of the countertorsion of the eyes is still debated [Wade and Curthoys, 1997 *Vision Research* **37** 1071–1078; Böhmer and Mast, 1999, in *Otolith Function in Spatial Orientation and Movement* Eds B Cohen, B J M Hess (New York: New York Academy of Sciences) pp 221–231]. However, other factors should be studied to clear up some discrepancies in the literature on this topic. The goal of the present research was to study the role of three factors: eye countertorsion, angular size of the stimulus, and gender of the participants. The results revealed that men showed a systematic E effect, whereas women presented an A effect. The increase of the angular size diminished the overestimation of the head tilt: in men, the E effect increased with small angular size; and in women, the A effect decreased but not enough to lead to an E effect. Preliminary analysis of the effect of countertorsion showed a significant link in the intra-variability between the countertorsion and the subjective vertical.

◆ **Reflex-like spatial updating can be adapted without any sensory conflict**

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Reflex-like processes are normally recalibrated with a concurrent sensory conflict. Here, we investigated reflex-like (obligatory) spatial updating (online updating of our egocentric spatial reference frame during self-motion, which is largely beyond conscious control). Our object was to adapt vestibularly induced reflex-like spatial updating with the use of a purely cognitive interpretation of the angle turned—that is, without any concurrent sensory conflict, just by presenting an image with a different orientation, after physical turns in complete darkness. The experiments consisted of an identical pre-test and post-test, and an adaptation phase in between. In all three phases, spatial updating was quantified by behavioural measurements of the new post-rotation orientations (rapid pointing to invisible landmarks in a previously learned scene). In the adaptation phase, visual feedback was additionally provided after the turn and pointing task (display of an orientation that differed from the actual turning angle by a factor of 2). The results show that the natural, unadapted gain of perceived versus real turn angle in the pre-test was increased by nearly a factor of 2 in the adaptation phase and remained at this level during the post-test. We emphasise that at no point was simultaneous visual and vestibular stimulation provided. We conclude that vestibularly driven reflex-like spatial updating can be adapted without any concurrent sensory conflict, just by a pure cognitive conflict. That is, the cognitive discrepancy between the vestibularly updated reference frame (which served for the pointing) and the subsequently received static visual feedback was able to recalibrate the interpretation of self-motion. [Supported by Max Planck Society and Deutsche Forschungsgemeinschaft (SFB 550).]

◆ **Modulating the synesthetic experience: A case study**

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In grapheme-colour synesthesia, graphemes cause the synesthete to see colours not present in the stimulus (photisms). The colour produced by a given symbol tends to remain constant over time. However, in a synesthetic subject, AED, we have identified a number of conditions that alter the vividness of the photism and/or cause shifts in brightness or hue. Based on AED's subjective ratings, the strongest photisms are elicited either by neutral (gray) characters, or characters coloured consistently with her mappings. Characters displayed in inconsistent colours make the photism less vivid. Further, for each grapheme, there is a region in colour space that eliminates the photism (the 'anti-colour'). The hue value of this anti-colour is highly correlated with the hue of the colour complementary to her normal synesthetic match ($r^2 = 0.91$). In a modified Stroop task, ink naming is slowed for graphemes displayed in a colour inconsistent with the photism. However, in trials in which the photism is eliminated or reduced because the grapheme is presented in the opponent colour, there is significantly less slowing. This suggests that the interference in the Stroop task is partly perceptual. However, a grapheme displayed in its anti-colour can produce a photism if there are multiple surrounding letters, and, more generally, the vividness of the photism of any grapheme increases when multiple graphemes are presented adjacent to one another. Surfaces are not necessary to produce a photism, as a cardboard sheet with letters cut out elicits a transparent colour percept in the plane of the hole. This photism is weakened if complex images with many colours are seen through the hole. Thus, the experience of the photism is not dependent only on recognition of the grapheme.

WEDNESDAY
POSTERS**MOTION—LOW LEVEL**◆ **Temporal properties of centre–surround interactions in human motion perception**

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A recent electrophysiological study revealed that the response to the antagonistic surround of macaque area MT receptive fields is delayed (15–20 ms) relative to the centre (Perge et al, 2002 *Investigative Ophthalmology & Visual Science* **43** E-Abstract 3931). We investigated whether this phenomenon, ie the delay between centre and surround, can be demonstrated in a human psychophysical experiment. The stimulus was a foveally presented circular patch of a moving random-dot pattern (centre) surrounded by a moving random-dot pattern annulus (surround). Stimuli in both centre and surround consisted of two-frame, single-step motion, repeated 6 times at 100 ms time intervals. The motion steps for the surround were presented earlier, simultaneously, or later than the centre (from –60 ms in 10 ms steps to +60 ms relative to the centre). The surround effect was quantified by measuring the strength of motion induction. Observers performed a direction-discrimination task for motion in the centre, with the surround moving in the same direction, or in the opposite direction. Performance was measured as a function of coherence level in the centre, always with maximum coherence in the surround. In accordance with earlier findings, motion induction was stronger at higher stimulus speed. Using this paradigm, we found the strongest surround effect at simultaneous centre–surround presentation. These results are in contrast to the electrophysiological results in area MT. This might indicate that short temporal delays between individual centre–surround receptive fields in the visual system are cancelled out at the level of perception.

◆ **Temporal integration for motion in central and peripheral view**

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Motion integrates over time, allowing even a weak signal in noise to be perceived given a long enough presentation. Temporal integration of motion, as measured by coherence thresholds, involves summation times greater than 1 s. Previous studies of motion integration have utilised relatively large motion stimuli. Some types of motion processing, however, show differences between centre and periphery. We tested whether the duration of temporal integration of translational motion is equivalent for centrally and peripherally viewed targets. The stimulus contained motion signals (limited lifetime of two frames) embedded in 4 s random noise, with stimuli viewed either centrally (3.5 deg circle) or peripherally (4–6 deg or 8–12 deg annulus). Direction discrimination was measured and coherence sensitivity determined for motion signals of varying durations (70–3500 ms). Linear integration of motion was found, with summation times ranging from 1 s to 2 s for all subjects and eccentricities. This similarity in integration times for varying eccentricities differs, however, from performance in which two separate motion signals are shown and the temporal delay between the two motion signals is varied.

◆ **Motion aftereffect of superimposed first-order and second-order motion**

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After looking at a moving pattern for a period of time, stationary (test) patterns appear to move in the opposite direction. Typically, this motion aftereffect (MAE) does not occur after adaptation to a second-order motion stimulus (ie motion defined by movement of a contrast or texture border, not a luminance border). Nevertheless an MAE of second-order motion can be perceived when using a dynamic test pattern instead of a static one. A ring-shaped stimulus was presented for 30 s (adaptation phase), in which a contrast modulation drifted on a carrier pattern of random dots, while the carrier pattern itself drifted in a direction opposite to the movement of the contrast modulation. Thus we have a first-order stimulus (the carrier pattern) and a second-order stimulus (the contrast modulation) superimposed. Afterwards, the test stimulus, either dynamic or static, was presented and the direction and duration of MAE for each was measured. To check the effect of attention, the experiments were also repeated under restricted attention condition (employing a visual digit discrimination task). The results showed that, although the adapting stimuli were the same for both static and dynamic tests, the direction of the static MAE tends to be opposite to the direction of first-order component of the stimulus, while the dynamic MAE tends to be opposite to the direction of the second-order component.

The results also pointed out that drawing attention away from the stimulus does not affect the direction and duration of the perceived MAE. Our results support the idea of separate processing pathway for first-order and second-order motion. The data we obtained also showed that, although attention is thought to be required in processing of second-order motion, drawing attention away does not affect duration of the perceived MAE.

◆ **Storage and the induced motion aftereffect**

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The motion aftereffect (MAE) has two components: adaptation is localised to the retinal region stimulated, and the subsequent expression of visual motion is global and dependent on the structure of the test stimulus (Wade et al, 1996 *Vision Research* **36** 2167–2175). This has been established with the induced MAE, in which motion can be perceived in a retinal region that has not been exposed to prior motion (Swanston and Wade, 1992 *Perception* **21** 569–582). It affords a method of distinguishing between local and global processes in MAE, and it is here applied to examining storage effects. All conditions in the experiment involved adaptation to two laterally moving gratings above and below (surrounding) a static central grating; during adaptation the central grating appears to move in the opposite direction and the surround appears static. The duration of the MAE in the central grating was measured with three static gratings. A control condition involved presenting the three static gratings on cessation of adaptation. Three storage conditions were presented for 5 s following adaptation and prior to the three static test gratings: central grating alone, surround gratings alone, or a blank screen. That is, the grating presented during storage could stimulate the region in which the MAE was seen (centre), that corresponding to the adapted region (surround), or neither of these. Fifteen observers were tested four times under each condition. MAE durations in all conditions (measured from the onset of three static test gratings) did not differ significantly. That is, storage was complete for all three conditions. This suggests that storage is not a function of the absence of retinal stimulation, but the absence of contours stimulating adapted and unadapted retinal regions.

◆ **Orientation selectivity of masking noises for chromatic and luminance motion stimuli**

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Noise can mask both detection and identification of motion. However, there have been few studies that compare the effects of different orientations of noise masks on motion perception. Here, we investigate the extent to which orthogonal noise masks motion identification. We measured thresholds for simple detection and for direction discrimination of a luminance or a chromatic drifting grating in the presence of either luminance or isoluminant chromatic 1-D noise. Luminance and chromatic gratings (1 cycle deg⁻¹) were composed by in-phase and anti-phase modulation of red and green sinusoidal gratings. We varied the contrast of 1-D dynamic luminance or isoluminant noise, superimposed on the grating either parallel or orthogonal to the motion direction. Our findings are: (i) Thresholds for both detection and direction discrimination of motion for isoluminant stimuli are constant in the presence of orthogonal luminance noise over the range of contrasts tested. The parallel luminance noise has little effect on detection thresholds but increases direction discrimination thresholds of isoluminant motion stimuli. (ii) Detection and discrimination thresholds for luminance gratings increase as parallel luminance noise contrast increases, whereas neither threshold is affected by orthogonal luminance noise. (iii) Parallel isoluminant chromatic noise influences motion discrimination and detection of the isoluminant stimuli but has less effect on the luminance stimuli. (iv) There is little effect of orthogonal chromatic noise on thresholds of either chromatic or luminance stimuli. We conclude that the orthogonal masking noise has little effect on the detection or identification of motion. The results are discussed in terms of possible oriented gain control mechanisms operating in the visual pathways. [Supported by NEI EY08300 grant to MJH.]

◆ **Measurement of the spatial-frequency tuning of second-order motion detectors with simultaneous masking in the absence of off-frequency 'looking'**

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Converging evidence suggests that, at least initially, first-order (luminance-defined) motion and second-order (contrast-defined) motion are processed independently in human vision. Additionally, adaptation studies suggest that second-order motion, like first-order motion, may be encoded by spatial-frequency selective mechanisms each operating over a limited range of scales.

However, the precise properties of these channels are indeterminate, and how spatial bandwidth and shape compare with those used to encode first-order motion is a fundamentally important issue. To address this issue we used an objective, bias-free, dual-masking paradigm to derive accurate estimates of the spatial tuning of these mechanisms, in the absence of off-frequency 'looking'. Modulation-depth thresholds for identifying the direction of a sinusoidal test pattern were measured over a four-octave range (0.125 to 2 cycles deg^{-1}) in both the absence and presence of two counterphasing masks, simultaneously positioned above and below the test frequency. For second-order motion, the bandwidths (half-height, full-width) of the resulting masking functions ranged from ~ 1 to 4 octaves, broadening as test spatial frequency increased. However, the general bandpass character of these functions remained relatively invariant with changes in centre spatial frequency, masking pattern contrast, and the temporal properties of the noise carrier. As expected, bandpass spatial tuning was also found for first-order motion. If, as some models suggest, first-order motion and second-order motion are encoded separately, our masking results provide compelling evidence that in each case the underlying mechanisms exhibit spatial-frequency selectivity. Thus, detection of first-order motion and second-order motion must utilise similar computational principles.

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◆ **Disambiguation of motion direction by first-order and second-order motion mechanisms**

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The display comprised 12 black dots arranged evenly around a virtual circle on a grey background. Half of these dots (every second dot) were displayed on one frame, followed by the other half after a suitable interval. This caused a sensation of ambiguous motion that could be either clockwise or counterclockwise on a particular trial. A continuous version of the display can be constructed by repeated cycling of the stimuli. We then interspersed lines between every second pair of points on intermediate frames. When the streaks were the same polarity as the dots (black), they disambiguated the direction of motion in the direction of the added streaks, as may be expected. However, for a wide range of dot-spacing and frame-rates, lines of opposite polarity disambiguated the motion in the opposite direction, against the positioning of the lines. For low frame-rates and large dot-spacing the white lines disambiguated in the direction of the motion. We explain the effects of the black lines and the inversion of motion direction caused by the white lines with a simple first-order model of motion detection: inverting the contrast produces motion energy of opposite direction. Facilitation of motion in the same direction by opposite-polarity stimuli (at longer distances and times) is consistent with a feature-tracking or second-order motion detection mechanism. A detailed model incorporating these two factors is presented.

◆ **Pitchfork bifurcations accompany hysteresis in the perception of apparent motion**

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Hysteresis is a well-documented phenomenon in the perception of apparent-motion patterns. Hysteresis is indicated when the initial percept persists despite changes of the stimulus that might result in the perception of an alternative percept. According to the mathematical catastrophe theory, hysteresis is always accompanied by divergence, or a pitchfork bifurcation. In the case of a pitchfork bifurcation, the percept disappears, and, instead of being replaced by a single other percept, it 'splits' such that it is replaced by one of two competing percepts. We present two experiments that show pitchfork bifurcations. Both experiments are based on the motion quartet paradigm, in which pairs of dots from diagonally opposite corners of an imaginary rectangle are presented in alternation with dots from the two other corners. Horizontal or vertical motion is perceived, depending on the aspect ratio—the ratio of height (vertical separation between dots) and width (horizontal separation) of the quartet. In the first experiment, the percept of stationarity was destabilised by gradually increasing the luminance contrast of the dots. In the second experiment, the percept of rotational motion was destabilised by gradually decreasing the frame duration of the display. In both cases, gradual parameter change resulted in the initial percept disappearing and splitting into competing states of horizontal and vertical motion. The relative frequency of the two motion directions depended on the aspect ratio of the quartet.

◆ **Bias in perception of ambiguous movement in discrete stimulus presentations**

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Successive presentations of two different stimulus configurations were used to generate a compelling but ambiguous apparent-motion sequence, such that the likelihood of the perceived motion being resolved as clockwise or anticlockwise was equal. In the first stimulus configuration, four small squares were arranged in a square formation ($5 \text{ deg} \times 5 \text{ deg}$) about a central fixation mark; in the second, they were arranged in a diamond formation. Twelve naïve observers reported perceived direction of motion in discrete presentations ($< 1 \text{ s}$), comprising three stimulus configurations (square–diamond–square; stimulus configuration duration 100 ms; ISI 200 ms). We were surprised to find that ten of the observers exhibited a strong bias for motion in one or other direction. This bias to report a particular direction persisted even when observers were informed of the inherent ambiguity of the stimulus. Next, in extended presentations (2 min) five observers indicated each occurrence of a perceived switch in direction. Despite individual variation, all observers reported switches in direction; an analysis of the interswitch durations conformed to a gamma distribution. These observations support the notion that uninterrupted presentations are required for perceptual switching to occur in ambiguous displays (Leopold et al, 2002 *Nature Neuroscience* **5** 605–609).

◆ **Does motion energy alone predicts salience from combination of motion and orientation contrast?**

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Motion perception can result from an interpretation imposed on figures perceived as segregated from the background at different locations and times (third-order motion, Lu and Sperling, 2001 *Journal of the Optical Society of America A* **18** 2331–2370). Alternatively, it can be based on the computation of motion energy, that is the extraction of velocity of spatiotemporal variation of light or contrast (first-order and second-order motion). Velocity of an oriented line, which is reflected by the orientation of space–time image, depends on absolute velocity (V_m) and on a component of velocity (V_o) modulated by the orientation (O) of the line (Adelson and Movshon, 1982 *Nature* **300** 523–525). We ask whether the salience (d') for a target displaying contrast of orientation (d_o : 0, 5, 7, 9, with respect to 45° -oriented background elements), velocity (d_{V_m}) or pairwise combination of these depends on: (a) either of these two salience components, (b) sum of individual salience components, (c) a salience mechanism responding to d_{V_o} only. d' was measured for d_{V_o} s corresponding to the different d_o s that increased or decreased d_{V_m} , depending on whether they were more orthogonal or more parallel than background elements. We showed that salience for more-parallel targets (in which d_{V_o} reduced d_{V_m}) was not accounted for by salience of either d_{V_m} or the $d_{V_m} + d_{V_o}$ sum but by the salience of a d_o mechanism, probably identified with third-order motion sensitive to orientation contrast. Salience for more orthogonal moving target (in which d_{V_o} increased d_{V_m}) did not depend on the salience of either dimension nor their sum—suggesting that it depends on salience of a d_{V_o} mechanism responding to orientation and motion direction conjointly at the earliest stage of motion energy computation (Casco et al, 2001 *Vision Research* **41** 275–284), which provides information about orientation of moving target, independently from the orientation processing in static viewing.

◆ **D_{\max} in the Fourier domain**

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D_{\max} , the threshold for motion direction discrimination with random-dot kinematograms (RDKs), gets worse as RDK displacement size increases. Feature-based models of motion explain this by pointing to the increased number of false matches caused by larger displacements. The analogous explanation in the Fourier domain is that increasing displacement creates an increasing number of lines of alias spatiotemporal energy. However, the Fourier explanation is complicated by the observation that increasing displacement simultaneously changes several other parameters of these alias lines (eg orientation, centre spatial frequency, interline spacing, etc). Computational and empirical investigation of these changes in relation to D_{\max} suggests that a number of spatiotemporal filter parameters need to be taken into account in order to explain D_{\max} in the Fourier domain.

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◆ Contrast normalisation in long-range motion processing

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The opponent energy output from the Adelson–Bergen model (1985 *Journal of the Optical Society of America A* **2** 284–299) can be normalised with the total motion energy (flicker energy) to yield a metric, motion contrast, which predicts performance on a direction discrimination task (Georgeson and Scott-Samuel, 1999 *Vision Research* **39** 4393–4402). Using a checkerboard stimulus with alternating checks containing either flicker or drift, we have investigated the properties of this normalising flicker energy and determined that it is bandpass in both spatial frequency and orientation (Rainville et al, 2002 *Vision Research* **42** 1727–1738). We investigated whether or not similar normalisation occurs for long-range motion stimuli (constructed by adding a 106 ms interstimulus interval between each frame of the original, short-range, stimulus). Intriguingly, normalisation was observed for these new stimuli, despite the fact that the motion-energy model does not account for long-range processing. Motion-contrast thresholds were higher than for short-range conditions. Manipulations of spatial frequency and orientation revealed differing patterns: for spatial frequency, the normalising flicker energy was still bandpass, as under short-range conditions, but more broadly tuned; for orientation, the normalisation was broadband, with no tuning at all. It appears that: (i) motion contrast can be applied usefully to stimuli analysed by either the short-range or long-range processes; (ii) normalising flicker has a greater effect under long-range conditions; (iii) normalising flicker is pooled selectively for short-range processing, but this holds only for spatial frequencies in the case of long-range processing—normalisation can occur across any orientation. This implies some commonality between the early stages in both the short-range and long-range motion processes.

◆ Visual search asymmetry for Brownian and ballistic motion trajectories

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Some stimuli in the world change direction on their own, while others move in ballistic trajectories, changing direction (and speed) only when they encounter obstacles. Both ballistic and Brownian motions are known to support efficient visual search when distractors are stationary (Royden et al, 2001 *Perception & Psychophysics* **63** 436–444). However, we do not know whether the visual system is preattentively sensitive to the difference between these types of trajectories. Ten observers were asked to detect Brownian targets among ballistic distractors and vice versa. Stimuli were light-gray disks (1.4 dva) on a dark-gray background. Brownian-motion stimuli changed direction every 27 ms, while ballistic-motion stimuli changed direction only to avoid the boundaries of the display. Set size was varied from 4 to 7 to 10 items. All stimuli moved at 8 deg s^{-1} . However, the apparent speed of Brownian stimuli was slower than that of ballistic stimuli, since the net distance traveled in the Brownian condition over any time interval longer than 27 ms was smaller than in the ballistic condition. Observers made speeded present/absent responses. Median RTs were divided by accuracy to correct for errors. One might predict that apparently faster ballistic motion would pop out against a background of apparently slower Brownian distractors. In fact, search for a Brownian target among ballistic distractors was markedly more efficient than search for a ballistic target among Brownian distractors ($10.7 \text{ ms item}^{-1}$ versus $34.6 \text{ ms item}^{-1}$). The ease of detecting Brownian targets among ballistic distractors suggests that changes in direction are visually salient.

◆ The effect of luminance upon perceived speed: Implications for Bayesian and ratio models

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It has previously been suggested that perceived speed may be computed by taking the ratio of two mechanisms that are differentially tuned for temporal frequency (Thompson, 1982 *Vision Research* **22** 377–380). Much psychophysical evidence is commensurate with such a scheme, including the finding that relatively slow, low-contrast patterns appear slower than high-contrast analogues, whereas fast low-contrast patterns may appear faster than high-contrast analogues. More recently, it has been suggested that perceived speed may be based upon a Bayesian model, whereby speed is derived from the product of a likelihood and a prior centred on a speed of zero (eg Hurlimann et al, 2002 *Vision Research* **42** 2253–2257). Both approaches make similar predictions for a range of stimulus attributes. In order to test the two models we have measured

perceived speed for patterns of unequal luminance. The results indicate that low-luminance patterns appear faster than higher-luminance patterns at high speeds (> 4 Hz) and veridical or slower at lower speeds. Thus, the effect of luminance upon perceived speed appears to be qualitatively similar to that of contrast. The results are not consistent with certain Bayesian models of human speed perception but may be reconciled with a ratio model.

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◆ **Judging speed in the periphery: Effects of contrast**

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It is well-known that reducing contrast can slow down the perceived speed of moving stimuli (Thompson, 1982 *Vision Research* **22** 377–380) and that moving stimuli in the periphery can appear slowed (Lichtenstein, 1963 *Journal of the Optical Society of America* **53** 302–306). We have investigated the effects of contrast reduction on perceived speed of stimuli in the periphery. Pairs of circular patches (2 deg diameter) of grating stimuli (all 2 cycles deg^{-1} with a standard rate of movement of 2 cycles s^{-1}) were presented simultaneously, one foveally the other horizontally displaced by 2, 4, 6, or 8 deg. Subjects reported which grating appeared to move faster. A staircase procedure determined the point of subjective equality of the two stimuli. Equal-contrast stimuli (both 0.1 or 0.7 contrast) and unequal-contrast stimuli (0.1 foveal, 0.7 peripheral; and 0.7 foveal, 0.1 peripheral) were investigated. Four subjects repeated all conditions eight times. The results show that for stimuli of equal low (0.1) contrasts, perceived speed dropped as the stimulus moved into the periphery, at least as far as 6° . For stimuli of high contrast (0.7) no such effect of eccentricity was found. For stimuli of unequal contrast, the 'classic' speed reduction effect was found at low contrast both in central and peripheral vision. Therefore the greatest mismatches were found when low-contrast gratings in the periphery were matched to high-contrast gratings in the fovea; speeds in periphery had to be increased by up to 60% to match the foveal stimulus.

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◆ **Context effects in categorisation of visual speed: A consequence of sequence dependences?**

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Category judgments of visual speed exhibit a systematic variability depending on which (low or high) speeds occur mainly at the outset of an experiment (the primacy effect) or with a greater overall frequency (the frequency effect) (Sokolov et al, 2000 *Perception & Psychophysics* **62** 998–1007). These effects are long-term, persisting as long as for at least 100 trials (eg Sokolov et al, 2002 *Perception & Psychophysics* **64** 561–569). Conversely, the sequence (contrast and assimilation) effects represent short-term dependences of the current judgment on psychophysical (stimulus/response) events that took place one to several trials in the past [eg Baird, 1997 *Sensation and Judgment: Complementary Theory of Psychophysics* (Mahwah, NJ: Lawrence Erlbaum Associates)]. Here, we examined if the primacy and frequency effects in categorisation of visual speeds arise from the sequence effects. An 'impulse plot' analysis [Lockhead, 1984, in *Preparatory States and Processes* Eds S Kornblum, J Requin (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 27–47] was applied to data sets obtained in a 2×2 factorial design: [frequent/infrequent] \times [low/high] visual speeds (3–9 deg s^{-1}) presented mainly on the initial trials and judged by participants who used three categories (slow, moderate, or fast). Impulse plots show the average judgment on trial T as a function of the particular speed or judgment presented k trials back. Despite the pronounced primacy and frequency effects observed with the overall mean judgments, the analysis failed to reveal any sequence effects in the four experimental conditions. Conversely, the impulse plots indicated systematic differences across conditions contingent on the particular frequency skew. The results suggest that the primacy and frequency effects in category judgments of visual speed do not derive from the short-term sequence dependences. Instead, they represent genuine effects induced by implicit experience with the statistical properties of experimental series.

◆ **Speed perception and wave theory**

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We address the question how changes in perceived speed affect reaction time (RT) to motion onset. We focus on the early stages of processing of speed information using barber-pole types of stimuli (crosses) differing in physical speed, length, and orientation. We measured choice RTs to left/right motion, and found that for objects moving at the same physical speed RTs increased when orientation of the bars approached the horizontal, as would be expected if the perceived speed determined the response. RT data were analysed by means of a procedure which aimed to separate sensorial from decisional components in a behavioural response. The procedure is derived from the functional model proposed by Bonnet and others [Bonnet and Link, 1998 *Analyzing Individual Differences in Reaction Time* (Québec: International Society of Psychophysics) pp 161–166; Bonnet and Dresch, 2001 *Psychologica* **28** 63–86], which in turn was developed from the ideas of the wave theory proposed by Link [1992 *The Wave Theory of Difference and Similarity* (Hillsdale, NJ: Lawrence Erlbaum Associates)]. Results show that orientation and length of the stimuli influences the sensorial component related to the computation of speed, at least in the early stages of processing. Our data support the idea that RT methodology is more adequate for investigating early stages of processing in speed perception than other traditional measures. [We are grateful to Claude Bonnet for his cooperation and insightful comments on this work. This research was partially supported by a grant from the Ministerio de Ciencia y Tecnología of the Spanish government (number BSO 2001-2008).]

◆ **A gradient-based model of the peripheral drift illusion**

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In the periphery, we see illusory rotation on a stationary radial grating with a sawtooth luminance profile (Fraser and Wilcox, 1979 *Nature* **281** 565–566). Eye movement causes actual retinal image motion (Naor-Raz and Sekuler, 2000 *Perception* **29** 325–335), but the percept of unidirectional motion is not fully explained. Faubert and Herbert (1999 *Perception* **28** 617–621) argued that motion detectors are activated because of the latency difference in the light and dark parts. Here we report new findings and propose a gradient-based account. First, an optimised stimulus can induce motion aftereffect on a stationary sinusoidal grating, which provides evidence for the activity of the visual motion mechanism. Second, perceived direction can be altered by background luminance. The local mean luminance seems crucial. On the basis of these findings, we propose that asymmetric responses of motion detectors to the jittering luminance gradient are the source of this illusion. A gradient model of motion detectors, which takes the image velocity as local temporal gradient over local spatial gradient, can predict such asymmetric responses if we assume imbalance in the positive and negative parts of temporal derivative filters. The asymmetry then depends on the DC offset of the stimulus, which explains the effect of the background luminance. The sawtooth stimulus is not optimal in this respect. Reported 'polymorphism' might reflect variability in subtle viewing conditions that could change the effective local mean luminance. We created a better stimulus by reversing the gradient direction in the positive-contrast and negative-contrast parts of the sawtooth grating so that the directional bias is always in one direction when the spatial and temporal derivatives are coupled together.

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◆ **Hysteresis in perceptual binding**

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Spontaneous alternations between perceptual motion coherence and incoherence occur during long lasting observation of 'aperture stimuli', reflecting the dynamics of neural activity with a single unchanging stimulus. We studied this phenomenon by registering the perceptual transitions between episodes of bound and unbound component motions using outlines of simple shapes viewed through apertures. Perceived coherence recorded continuously for 60 s with an analog device for four different contrast levels shows that the mean duration of episodes of perceived coherence (4 s) increases with decreasing contrast. Perceptual alternations induced at a slow rate (0.05 Hz) by smoothly changing parameters known to influence motion binding (contrast, aperture visibility, form) further reveal the existence of a perceptual hysteresis, suggesting that competitive/cooperative mechanisms are involved. Additional experiments with fixed durations of

motion (100–1600 ms) and varying contrasts (10%–70%) indicate that motion integration is fast and has a high contrast sensitivity, whereas segmentation is slower and has a poorer contrast sensitivity. These different dynamics may account for the asymmetry observed in perceptual hysteresis and could reflect the distinct contributions of the magnocellular and parvocellular pathways to form/motion binding.

◆ **Smooth-pursuit latency does not affect perceived plaid direction**

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Some Type II plaids are perceived in the vector average (VA) direction as opposed to the intersection of constraints (IOC) direction at short durations or at low contrast. Both of these observations are consistent with an effect of the initiation of the smooth-pursuit response. In support of this interpretation, Masson and Castet (2002 *Journal of Neuroscience* **22** 5149–5163) provided evidence that there was a transition from Fourier to non-Fourier tracking in the eye movements of subjects viewing plaids. To eliminate the possible effects of smooth pursuit on perceived plaid direction, the gap effect was employed to modify the latency of smooth-pursuit eye movements. In the current study there were three levels of stimulus duration and four levels of pre-stimulus gap duration. A forced-choice clockwise–anticlockwise task was used to determine perceived plaid direction. The results showed an effect of duration as previously reported (Yo and Wilson, 1992 *Vision Research* **32** 135–147) but no effect of smooth-pursuit latency. The size of the stimulus was varied to prevent locking of the smooth-pursuit system and the results were similar. The results have shown that manipulating the smooth-pursuit system by using the gap effect does not affect perception of plaid direction. This result is interesting in light of the work of Masson and Castet.

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EYE MOVEMENTS AND PERCEPTION

◆ **Tracking eye movements while reading: Printing press versus the cathode ray tube**

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The most common finding is that reading speed is slower for screen-presented text versus paper (Dillon, 1992 *Ergonomics* **35** 1297–1326). However, owing to a great disparity in procedures, and a number of confounding variables, evidence for a speed deficit in reading from screen remains inconclusive. Moreover, few studies have dealt with possible differences in eye-movement patterns between these two media. In this study, we compared normal reading speed (words per second), comprehension, and eye-movement patterns (forward fixations, regression, re-fixations, and undershooting) for text presented on paper versus text presented on screen. We also manipulated line length (70 and 110 characters per line), for studies have shown that longer line lengths on screen increase reading speed, but decrease comprehension (Dyson and Haselgrove, 2001 *International Journal of Human–Computer Studies* **54** 585–612). In an attempt to make the two modes of texts similar, we controlled for visual angle, distance, text angle (both at 90°), text length, font, font size, and text border. Subjects also answered a brief questionnaire regarding their computer and Internet use. Overall, results showed no statistically significant difference in reading speed, comprehension, or eye-movement patterns between these two media, and line lengths. As expected, computer experience and use (especially for reading news online), was positively correlated with reading speed for text presented on screen. Interestingly, although the majority of subjects indicated that they preferred reading text from paper, the difference in reading speed between screen and paper was positively correlated with computer experience and use, with more experienced users performing quicker in the screen condition, and less experienced users performing quicker in the paper condition.

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◆ **Reading with a central visual scotoma: Synchronising the eye movement and the availability of visual information**

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Reading with a central visual scotoma disrupts the motor and cognitive processes of reading. We studied a procedure for improving the quality of reading by patients who have central scotoma by coordinating the visual and cognitive performances of the patients with their handicap.

The maintenance of eye programming in a central reference area and the presence of all visual information related to the word, to avoid any investigation of the word in a peripheral retinal zone, could improve the performance of reading. Therefore we suggest synchronising the eye movement and the availability of visual information by unmasking the visual information present under the scotoma. We tested this hypothesis during the reading of texts by healthy subjects with a simulated central scotoma of different sizes. We compared the performance and the strategy of reading when the scotoma hides letters (pathological condition), during the immediate unmasking on both sides of the scotoma, and without the presence of scotoma. Our results show that spatial destructuring of a word by unmasking the letters perturbs the quality of reading. The slightest decrease of speed during reading when the scotoma hides letters shows the importance of the morphological cue of the word during dynamic reading or even with the presence of a visual scotoma. The new proposal involving the unmasking of information by respecting the morphological cues of the word and spatial cue of the text (space) is being investigated.

◆ **Reading without a fovea: Effects of the location of a pseudofovea on reading performance**

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In patients with macular degeneration, the central visual field can no longer be used for tasks like reading or object recognition. In order to regain abilities in these tasks, patients often use the strategy of constantly looking to the side of the object they currently want to see. At the level of the retina, this location was termed 'pseudofovea'. The present study was designed to investigate the effect of the location of this pseudofovea on reading performance. Healthy participants had to learn to read with a simulated inverse scotoma; text was presented in a blurred way, with only a small cut-out with a constant offset from the current measured fixation for seeing the text clearly. Therefore, participants had to use the same strategy as patients with macular degeneration in order to be able to read the text. The effect of the location of the cut-out (the simulated pseudofovea) on reading performance was investigated. In experiment 1, the cut-out was either to the left or below the fixation. Reading performance (words per minute, number of fixations) was better when the cut-out was to the left of fixation. In experiment 2, in which reading performance was compared when reading with the cut-out on the left versus being on the right, an advantage was found for the cut-out on the right. In addition to the differences in reading performance, clearly distinguishable fixation patterns were observed. So far, it is unclear whether the findings depend on the text being presented from left to right. Therefore, an investigation is in progress with the object of finding whether the same patterns occur when text is presented from top to bottom.

◆ **Do object viewing strategies change when parts are ambiguous?**

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Part-based theories of object recognition have been around for nearly 20 years (Biederman, 1987 *Psychological Review* **94** 115–147) and there is recent evidence for part-based attention (Vecera et al, 2001 *Perception & Psychophysics* **63** 308–321), but viewing strategies in object-identification tasks have not been studied. What strategies do subjects employ when identifying objects? How are these strategies affected by the appearance of parts? We investigated these questions with a word-identification task. The horizontal and vertical eye positions of subjects were measured with the SRI Dual Purkinje Image Eye tracker. Words were presented with letters subtending 1 deg to create a closer analogy to object-identification tasks. Subjects returned to a central fixation marker after identifying the word that appeared in a random location. Four word conditions were used: unmasked (control), front, middle, and end-masked. In the control condition, subjects were able to identify the word in ~1 s. In all conditions, subjects first fixated at 35% of the word length, consistent with the optimal word-reading location [O'Regan, 1992, in *Eye Movements and Visual Cognition: Scene Perception and Reading* Ed. K Rayner (New York: Springer) pp 333–354]. When the central region was masked, the fixation pattern was identical to that of the control condition, but dwell times increased by 50%. When the beginning and end regions were masked, additional fixations were made at 20% and 80% of the word length, respectively. We concluded that first fixations fall on the most semantically meaningful part of the object—in our case, the root of the word. When the appearance of parts outside the fovea is inconsistent with the object hypothesis, subjects modify their strategy to include a fixation in the ambiguous region.

◆ **Predictions of eye movements based on tracked previous locations and salience measures**

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We present a model for predicting the eye movements of observers viewing dynamic sequences of images. As salience measure we have evaluated an invariant of the spatiotemporal structure tensor that indicates an intrinsic dimension of at least two. This salience is used to derive a list of candidate locations. Out of this list, the currently attended location is selected according to a mapping found by supervised learning. The true locations used for learning are obtained with an eye-tracker. In addition to the salience-based candidates, the selection algorithm uses a limited history of the tracked locations attended in the past. The mapping is linear and can thus be quickly adapted to the individual observer. The mapping is optimal in the sense that it is obtained by minimising, by gradient descent, the overall quadratic difference between the predicted and the actually attended location. Many efforts have been made to understand the scan path of observers that view static images. We believe that, with a dynamic visual input, the eye movements are easier to predict because random and top-down influences may be less. Still, different observers can have very different scan paths and, therefore, see different things with the same visual input. For this reason, we have designed a model that can be tuned to a particular observer. For the same reason, we decided to not only observe the scan path but to change it such as to improve visual communication and vision-based interaction (see <http://www.inb.uni-luebeck.de/Itap>). Our model will help to do that.

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◆ **Local contrast affects fixation density in saccadic search**

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In saccadic search, the visual span is the area from which information is extracted during a single fixation. Näsänen et al (2001 *Vision Research* **41** 1817–1824) reported that the size of the visual span depends on the contrast between stimulus elements and background (high contrast → large span, low contrast → small span). On the basis of this finding, we expect fixation density to vary across a stimulus having areas with different element-background contrasts. To investigate fixation density we adopted the Voronoi tessellation method of Over et al (2002 *Perception* **31** Supplement, 182). Subjects were instructed to search for a closed symbol amongst Cs (81 elements in total). In three conditions stimulus contrast was manipulated: (a) uniform low contrast, (b) uniform high contrast, and (c) mixed contrast (stimulus was separated in three strips of low, medium, and high contrast). With the Voronoi tessellation method we quantified the homogeneity of the spatial distribution of fixations in one single parameter, α . α was similar for the spatial distribution of fixations in the conditions with uniform contrasts. As expected, the spatial distribution of fixations was less homogeneously distributed in the mixed-contrast condition. Fixation density decreased with increasing local contrast. We find that (i) size of the visual span (modified by contrast) affects the fixation density; and (ii) the Voronoi method is a useful technique for studying saccades in relation to variations in the size of the visual span.

◆ **Determining relative positions across a saccade: Not a comparison of independent judgments of position**

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During smooth-pursuit eye movements, subjects judge the distance between objects on the basis of their separation in the retinal image and not on the basis of their actual separation (Brenner and Cornelissen, 2000 *Vision Research* **40** 2557–2563). In this study we examined the extent to which this is also true for saccadic eye movements. Do subjects consider that the eye has moved when they determine the separation between a target flashed before and another flashed after a saccadic eye movement? Subjects were asked to track a jumping dot with their eyes. While they did so, we flashed two targets, with a 67 ms interval between them, at predetermined retinal positions. After each trial, subjects indicated the perceived screen positions of the two targets. We selected trials on which subjects made a complete saccade in between the presentation of the

two targets. These trials were compared with ones in which the eyes were fixating between the presentation of the two targets. There was a strong correlation between the errors in judging positions of the two targets. This was so when a saccade was made between the presentation of the two targets as well as when no saccade was made. The variability was also only about half as large for the set separation between the two targets as the error in judging the position of a single target. Thus, subjects judge relative positions directly rather than judging relative positions on the basis of independent judgments of the positions of the components. Nevertheless, the set separation itself was influenced by the saccade. Subjects did not simply reproduce the retinal separation as they had done during pursuit. The judged separation was far from veridical though: subjects underestimated the separation considerably. Thus, subjects only considered a small portion of the saccadic amplitude.

- ◆ **Contrast response function and spatial summation area of human short-latency ocular following**
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Short-latency ocular following responses in humans involve spatial integration of motion signals across the visual field. We investigated the contrast response function and the spatial summation area of these responses, for both grating and pattern motion. Movements of the right eye were recorded by the scleral search coil technique (three subjects: two authors, one naïve). Vertical moving gratings ($0.27 \text{ cycle deg}^{-1}$, 10 Hz) or unikinetic plaids (the sum of a vertical, moving grating, and an oblique, static grating of same SF) were briefly presented (200 ms) on a large ($70 \text{ deg} \times 70 \text{ deg}$) projection screen, within a circular window (diameter: $2.5\text{--}20 \text{ deg}$). Luminance of the display was carefully calibrated. Mean background luminance was of 12.5 cd m^{-2} . The total contrast of gratings and plaids was varied from 2.5% to 80%. Increasing the contrast of a moving grating reduced the latency and increased the amplitude of the earliest tracking responses. Contrast response functions showed a steep increase (half saturation, $\sim 10\%$) followed by a plateau. Increasing the size of the stimulus induced a strong increase in the response amplitude for radius up to $\sim 10 \text{ deg}$, followed by a plateau. Spatial summation functions were independent from contrast. Unikinetic plaids elicited an early ($\sim 85 \text{ ms}$) component in the grating motion direction and a late ($\sim 110 \text{ ms}$) component in the pattern motion direction. These components showed different half-saturation contrast values of $\sim 10\%$ and $\sim 20\%$, respectively. These results unveil the spatial properties of a ‘functional receptive field’ for the initiation of tracking eye movements.

- ◆ **Eye movements in natural scenes**

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Eye movements in scenes recorded in laboratory conditions are known to be influenced by factors such as scene structure and instructions to the observer. The aim of this work was to investigate how eye movements recorded in out-of-doors natural scenes relate to spectral and spatial structure. Accordingly, eye-position data were recorded from observers in stationary urban and rural environments with a modified infra-red *xy*-gaze-tracking device which uses the pupil and corneal reflection (iView, SensoMotoric Instruments GmbH; sampling rate 60 Hz; angular resolution 0.2 deg). Hyperspectral data were also obtained from the same scenes over the range $400\text{--}720 \text{ nm}$ at 10 nm intervals (Nascimento et al, 2002 *Journal of the Optical Society of America A* **19** 1484–1490). Observers were instructed to look at the scene for 5 min so that they could answer a question about its composition afterwards. Eye-position data were analysed off-line and in relation to the spatial distribution of spectral radiance in the scene derived from the hyperspectral data. Despite some variation between observers, a common map of fixations emerged. In particular, low-luminance regions in the scenes were looked at with low probability and extended edges defined a consistent guide for fixations.

- ◆ **Schemas influence the time course of attention allocation to complex natural scenes**

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According to previous research, schemas mediate attention allocation across a scene and memory for the elements in that scene (Brewer and Treyns, 1981 *Cognitive Psychology* **13** 207–230; Friedman, 1979 *Journal of Experimental Psychology: General* **108** 315–355; Goodman, 1980 *Cognitive Psychology* **12** 473–495). However, the time course of such effects remains uncertain. While their eye movements were monitored, observers viewed photographs of an action performed by an actor. Objects in each scene were pre-classified as of high or low relevance to the action. Afterwards

memory was tested for objects from each scene. Dwell times and number of fixations were significantly higher for low-relevance items, suggesting that covert attention allocation is affected by object relevance. Recall showed the expected advantage for retrieval of high-relevance objects, while recognition was superior for low-relevance objects. Further analyses revealed that these attention allocation effects were not consistent across the viewing period. The ordinal positions of fixations on high-relevance objects were generally lower than for low-relevance objects. Time course analyses confirm and qualify this result. Early in viewing time there was a preponderance of fixations on high-relevance objects, but soon afterwards fixations were heavily biased towards low-relevance items within the scene. This pattern of results is consistent with an initial attempt at scene comprehension, closely followed by attempts to dis-confirm and/or integrate irrelevant material with the initial understanding of the scene.

◆ **Eye movements in an information search task**

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Information retrieval from the web has increased noticeably and scanning search results from different search engines is a quite usual task. In an information search task, we recorded subjects' eye movements, when they searched for a target in a list of article titles. The lists consisted of twelve news headlines. 75% of the trials were target-present trials in which there was one relevant title in the list. In 25% of the trials the relevant title was absent. The relevant title was located equally often in the beginning (titles 1–4), in the middle (titles 5–8), and in the end of the list (titles 9–12). After finding the target, the subjects pressed a button and reported which of the titles corresponded to the question. Preliminary results indicated that the mean fixation durations were longer and there were more fixations per word when the target title was absent. We suggested that more careful search and processing were needed when the target was absent. The effect of the target position was also significant: there were fewer fixations per word, and more words per second were read when the relevant title was in the beginning of the list. Interestingly, there were more fixations per word when the relevant title was in the middle of the list than when it was at the end of the list. This might indicate that the subjects had to scan the whole list before they could decide whether they had found the relevant title from the middle.

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◆ **Eye-movement strategies in a size comparison task**

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Saccades serve the visual system by bringing areas of interest to the central part of the retina. Which saccade strategy is used if visual information is presented at two different locations? We investigated the eye-movement strategy by manipulating actual and expected detectability of the information. Subjects had to decide, as fast as possible, whether two squares had equal sizes. Each square could be large or small. The squares were separated 15 deg at 10° eccentricity (left, right, up, or down) relative to the starting position. In four conditions, the visibility of the squares was manipulated by varying the contrast between the squares and the background (the more visible the less difficult). Subjects were allowed to move their eyes. Trials from the four conditions were presented both blocked and mixed. Subjects used several scan strategies: (i) no saccade; (ii) one saccade that ended between the squares; (iii) one saccade to one of the squares; (iv) (repeated) fixation of both squares. Strategy (i) occurred mainly in easy trials, strategy (iv) mainly occurred in difficult trials. In blocked trials, the reaction time, the number of saccades, and the amplitude of the first saccade increased with decreasing visibility of the squares. Surprisingly, in mixed trials both the reaction time and the amplitude of the first saccade were similar for all four conditions. The use of the different strategies was less pronounced in mixed trials than in blocked trials. We conclude that subjects use visual information of the current trial and knowledge from prior trials to adjust saccade parameters and scan strategy to the demands of a visual comparison task. These adjustments are not necessarily optimal.

◆ **Influence of the reference frame for action in the orienting of attention**

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The present experiments focus on the relation between the coordinate system used in the planning of saccades directed to a new object or within the same object and the orienting of attention. Subjects executed sequences of visually guided and memory-guided saccades towards

one long or two short objects occupying the same space. Different coding for inter-object and intra-object saccades was found. The former are coded in retinocentric coordinates and updated with respect to the eye position to aim for a precise position in the new selected object, while the latter are coded in oculocentric coordinates as a fixed motor vector applied irrespective of the initial landing position on the object. This demonstrates that the reference point for action for saccades aiming for a new object differs from that for exploring the same object. We examined whether a different perceptual process could depend on these different reference points for action. Indeed, a growing body of evidence shows that the selection of a new object for the saccade target influences the orienting of attention. The selection of the saccade target results in this location being processed preferentially at the expense of others. Such a relationship was examined here in the case of inter-object and intra-object saccades, to assess the role of the reference point used for the saccade in attentional selection. Overall, our results show that the coupling between the selection for perception and saccade depends on the reference frame used for the saccade.

◆ **Is there a relationship between saccadic compression and saccadic suppression?**

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During saccades, briefly presented visual stimuli with low contrast are often not perceived (saccadic suppression). Stimuli with high contrast, on the other hand, are perceived during a saccade but yield errors of apparent position. Apparent position is often compressed toward the saccade target. Interestingly, saccadic suppression and saccadic compression have very similar time courses (Ross et al, 2001 *Trends in Neurosciences* **24** 113–121). They begin 50 ms before the saccade and reach a maximum at saccade onset. Moreover, a recent neurophysiological study (Krekelberg et al, 2003 *Neuron* **37** 537–545) indicated that saccadic compression may result from changes in firing activity of cortical neurons that are induced by saccadic suppression. A possible link between compression and suppression was investigated by measuring both simultaneously as a function of stimulus contrast. Three subjects conducted horizontal saccades (20°) over a grey computer screen. Around the time of the saccade a light bar was flashed for 7 ms at one of four possible positions. The contrast of the bar could have one of five values: 0.04, 0.07, 0.14, 0.27, and 0.64. Subjects had to report whether they perceived the bar and, if yes, had to indicate its apparent position with a mouse pointer. The strength of saccadic compression and the strength of saccadic suppression both increased with decreasing contrast of the stimulus. It was also confirmed that the time course of suppression and compression was similar. It is concluded that saccadic compression may be associated with saccadic suppression.

◆ **Trans-saccadic temporal integration of motion**

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How is visual information combined across separate fixations? We studied the temporal integration of two brief (150 ms) motion signals embedded in 10 s noise, measured by motion-coherence thresholds. Full temporal summation of motion was found to occur when the interval between the two motion signals was as large as 2 s. When a saccadic eye movement was made during the trial, motion summation occurred only when the locations of the two motion signals were either spatiotopically or retinotopically matched. Motion integration occurred across saccades even when each individual motion signal was, by itself, below detection threshold. Further experiments showed that integration was mediated by attention. The finding that important congruent visual information builds up trans-saccadically, while irrelevant noncongruent information fades, could provide a simple and robust strategy to solve the problem of instability of the world during eye movements.

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◆ **Time course of intrasaccadic reduction of contrast sensitivity: Horizontal versus vertical gratings**

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Contrast sensitivity for a horizontal low-spatial-frequency grating displayed during a horizontal saccade is strongly reduced. This sensitivity reduction is maximal at saccade onset and decreases thereafter (Diamond et al, 2000 *Journal of Neuroscience* **20** 3449–3455). We investigated whether the same time course is observed with static vertical gratings flashed on the screen. We measured the ability to detect a low-spatial-frequency grating ($0.18 \text{ cycle deg}^{-1}$) flashed (12 ms) on the upper or lower part of a screen during horizontal voluntary saccades (amplitude: 6 deg). Observers indicated, by pressing one of two buttons, the part of the screen in which they perceived the grating

(spatial 2AFC). Grating orientation was vertical or horizontal, contrast was constant (4% or 5% depending on observers) with a mean luminance of 18 cd m^{-2} . Off-line analysis of ocular movements allowed us to assess the temporal relationship between the grating and the saccade on each trial. We found that maximum reduction of performance occurs when the grating appears just after saccade onset, thus confirming Diamond et al's results. The pattern of results was the same, whatever the orientation of the grating (vertical or horizontal). Whereas a static vertical grating flashed during a horizontal saccade produces high retinal temporal frequencies, an intrasaccadic horizontal grating does not induce any retinal motion. Consequently, if the magnocellular motion-detection system was selectively inhibited during saccades, contrast sensitivity should be more reduced with the vertical grating than with the horizontal one. Our results, however, are not consistent with this hypothesis.

◆ **How visual landmarks affect the detection of stimulus displacement across saccades**

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Displacements of visual stimuli during saccades are often not noticed. We have demonstrated that this saccadic suppression of displacement can be eliminated by blanking the stimulus for a short period during and after the saccade, and that continuously present objects serve as landmarks for postsaccadic relocalisation (Deubel et al, 1996 *Vision Research* **36** 985–996; Deubel et al, 2002 *Progress in Brain Research* **140** 165–180). Here, we study in detail the effect of the spatial and temporal characteristics of the landmarks on perceived transsaccadic shift of a saccade target. In a first experimental series, landmark locations with respect to the target were systematically varied. The data show that landmarks close to the saccade target and horizontally aligned with the target are especially effective. In the second type of experiment, we varied the delays of target and landmark presentations after the saccade. The data reveal a striking 'first come, first served' rule: the stimulus that precedes for only a few milliseconds is taken as a landmark for postsaccadic relocalisation. This effect largely remains, even if target and landmark appear as late as 400 ms after the saccade. Third, we studied how the contributions of more than just a single landmark are integrated for postsaccadic localisation. The findings are compatible with a model that assumes spatial references are determined by the centre of gravity of the individual landmarks, weighted by their distance to the target.

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◆ **Saccades and localisation judgments with briefly presented stimuli**

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When observers are asked to localise the peripheral position of a probe with respect to the midposition of a spatially extended comparison stimulus, they tend to judge the probe as being more peripheral than the midposition of the comparison stimulus (Müsseler et al, 1999 *Perception & Psychophysics* **61** 1646–1661). To explain this finding, I examined a model that postulates that in the calculation of perceived positions two sources are involved, a sensory map and a motor map. The sensory map provides vision and the motor map guides saccadic eye movements. The model predicts that errors in location judgments will be observed when the motor map has to provide the information for the judgments. In several experiments, I examined, and found evidence for, this prediction.

◆ **Recognising snapshots in two visual modes**

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Models of perception and action often propose two systems of visual processing, one variously named pre-attentive, ambient, or dorsal; and the other attentive, focal, or ventral [eg Ungerleider and Mishkin, 1982, in *Analysis of Visual Behavior* Eds D J Ingle, M A Goodale, R J W Mansfield (Cambridge, MA: MIT Press) pp 549–586; Norman, 2001 *Behavioral and Brain Sciences* **24** 73–137]. However, this distinction has never been associated with eye movements. In recent studies, we obtained evidence that eye-movement parameters are indicative for each of the two processing modes. The crucial feature of their differentiation was the combination of fixation duration and the amplitude of the previous and following saccades (Velichkovsky et al, 2002 *Transportation Research, Part F* **5** 145–156). In a further experiment, we tried to validate these eye-movement parameters by testing theoretical assumptions about memory representations related to each of the two modes. After a short presentation of various real-world pictures, subjects had to recognise cut-outs of these pictures, which were selected according to their fixation locations.

Results indicate that cut-outs presumably processed in ambient mode are less well recognised than cut-outs which were processed in focal mode. The findings are presented and discussed in the framework of the two-visual-systems approach.

◆ **Effects of expansion and contraction of stimulus image on vergence eye movements**

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Changes in a target distance produce changing parallax, which induces vergence eye movements. Changes in the distance also produce information about expansion/contraction of the target image on the retina. We examined the effect of expansion/contraction of stimulus image on the dynamics of vergence eye movements. To do this, we used stereoscopic stimulus that provided information about changing parallax and expansion/contraction independently. The results were as follows. (i) Velocity of vergence eye movements was higher when stimulus information about changing parallax and expansion/contraction both provided identical directional information of distance change than when they provided conflicting directional information. However, we also showed that expansion/contraction without changes in parallax hardly elicited vergence eye movements. (ii) When a stimulus in horizontal position was yoked to each viewing eye (visual feedback loop of the horizontal stimulus position was open), convergence eye movements occurred whenever stimulus changed in size, regardless of expansion or contraction. Velocity of convergence was, however, higher when the stimulus expanded than when it contracted. (iii) When the stimulus provided information about expansion/contraction simultaneously with changing parallax, this produced higher velocity of convergence eye movements than when there was no expansion/contraction information. These results imply that the oculomotor system obtains information about expansion/contraction of stimulus image to drive the vergence eye movements, but the system does not use the directional information from expansion/contraction. On the basis of these results, we propose a model of vergence eye movements that makes use of information about expansion and contraction of stimulus image.

◆ **The return of eccentricity effects on saccade latency—effects of cues and expectancy**

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When subjects make saccades towards targets presented on an unstructured visual background with eccentricities in the range 1° – 12° , saccade latency is independent of eccentricity. However, Hodgson (2002 *Experimental Brain Research* **145** 539–542) recently demonstrated that eccentricity effects are observed when structure is provided in the form of markers for the locations of saccade targets. The effect of target presentation time, a focusing cue, and expectancy has now been investigated. Subjects viewed a visual display from 57 cm with their heads stabilised. After a variable fixation period, a cue circle (radius 4.5°) centred on the fixation target appeared. After a variable SOA (150 ms–300 ms) the saccade target appeared randomly to the left or right at 3° , 6° , or 9° for either 20 ms or 200 ms. On 59% of trials the targets appeared at 3° , 12% at 6° , and 9%; the remaining trials had either no cue (target 6°) or a cue but no target. In control runs, targets appeared (display time 200 ms) with the variable probability distribution but no cue, or with a cue but equal probability of the target appearing at each of the eccentricities. Eye movements were recorded by infrared oculography and saccade latency measured offline. There was a pronounced eccentricity effect in runs with both cues and variable probability, which was largest for a target presentation time of 200 ms (eg 20 ms: left 3° , 225 ± 5 ms; 9° , 241 ± 8 ms; 200 ms: 3° , 174 ± 2 ; 9° , 221 ± 4.2 ms; mean \pm SEM). A smaller eccentricity effect was present with variable probability, and the smallest effect was observed with the cue alone. These results support the hypothesis that saccade latency is related to eccentricity when internal and external cues are present, as might occur in actual behaviour in cluttered visual environments.

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OBJECTHOOD

◆ **Collinearity and target – nontarget congruence in perceptual grouping**

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In this study, the effects of collinearity, spatial proximity, and target–nontarget congruence on perceptual grouping were distinguished. A global shape was interpolated between Gabor patches of a target spatial frequency in a field of distractors. Response times to the orientation of the global shape were measured (2AFC or 4AFC). Different relational information types were varied

in the experiments. These included part–part relations, such as sameness in orientation and spatial proximity between the patches, as well as part–whole relations, such as alignment of the patches to the whole and part–whole orientation congruence. Distinguishing between part–part and part–whole relations, sameness of patch orientation provided facilitation only at small between-target distances, while alignment facilitated at both small and large distances, in spite of interspersed distractor patches. Distinguishing early from late part–whole effects, a double dissociation of alignment and part–whole orientation was obtained in two experiments. The results could be interpreted as evidence for contour interpolation as an early perceptual mechanism combining parts into a global whole.

◆ **Collinear suppression**

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Contextual elements in the neighbourhood of a target element can modulate human psychophysical as well as neural responses to this target. In almost all studies up to now, collinear contextual elements have been found to improve target perception and neural firing rates—in accordance with the Gestalt law of good continuation. Using the recently discovered shine-through effect, we show here that, contrary to these previous investigations, collinear contextual elements can strongly suppress target perception when target processing is limited by backward masking. For unmasked targets no suppression is found. It seems that the benefits of collinear contextual elements have to emerge in a long-lasting process. We argue that collinear processing is preceded by grouping operations that suppress collinear targets on the first processing stage after stimulus onset. By varying the onset and duration of the collinear contextual elements, we reveal the transient nature of this grouping and collinear processing.

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◆ **Phenomenal stratification of bidimensional coloured surfaces induced by edge movement**

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The aim of the present study was to reconsider and further explore the visual occlusion effect induced by motion of the boundary between two juxtaposed surfaces of different colour (Sampaio, 1943 *Studia Psychologica* 277–298). Two kinds of boundary movement—translation and deformation—have been investigated. Different computer-generated kinematograms were produced to explore the perceptual effect of occlusion. In the case of edge translation, the horizontal displacement of the boundary does not change its shape, while the areas of the juxtaposed surfaces do change. In the case of edge deformation, the shape of the boundary changes in time while the areas of the two surfaces are kept constant. When the motion was a horizontal edge translation, in both right-to-left and left-to-right directions, observers perceived occlusion. Instead, in the case of the edge deformation, in which the motion was due to a continuous change of the shape of the two regions of different colour, observers perceived juxtaposition. These results, which only partially agree with those of Sampaio, are discussed in relation to the literature on both amodal completion and visual overlapping phenomena.

◆ **Competition and integration in monocular rivalry**

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The paradigm of monocular rivalry (MR), also called pattern rivalry, has been used to illustrate selective suppression of one of two superimposed visual patterns or images. Much like the related phenomenon of binocular rivalry (BR), perception during MR is dynamic, and often marked by dominance of only one of the competing patterns, with complete invisibility of its rival. However, MR distinguishes itself from its counterpart in that it arises in the absence of any interocular conflict, but is highly restricted in the types of stimuli that will engage in spontaneous alternation. Here we report several experiments that attempt to identify the principles by which perception selects and/or suppresses superimposed patterns during MR. Stimuli generally consisted of superimposed orthogonal gratings, which have been shown previously to engage in vigorous rivalry. However, in the present study, some of the patterns were complete, covering the extent of the stimulus, while other patterns were ‘partial’, covering only a portion of the stimulus (eg containing a blank window). Superimposing complete and partial stimuli provided a heterogeneous MR stimulus, with some regions containing pattern conflict and others containing only one pattern. We report that, upon viewing these stimuli, perceptual dominance of a partial

pattern often entailed the complete suppression of its rival, even in those regions (up to several degrees in size) devoid of local competition. These results illustrate that, in resolving perceptual conflict, the brain dissects a superimposed stimulus according to inferences regarding the global structure of the competing patterns. Additional experiments revealed similar results with complete and partial competing patterns during BR.

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◆ **The time course of visual feature binding**

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How the various features of an object are bound to a coherent percept is one of the puzzling problems in the cognitive and neural sciences. While most of the discussion focuses on the neural mechanisms underlying feature binding, less attention is paid to the spatial and temporal characteristics of the process itself. To investigate the time course of feature binding, we used the recently discovered feature inheritance effect: a shortly presented vernier remains invisible if followed by a grating comprising five straight elements. Surprisingly, the offset of the vernier is perceived at one of the edges of the grating—even though the vernier itself was displayed at the centre. Hence, vernier offsets can be freed from their carriers. These freed features can be fused with real offsets of one of the edge elements of the grating. In the experiments, this offset was anti-offset, ie in opposite direction to the vernier. We varied the onset and duration of this anti-offset. With this setup we show that: (i) feature binding lasts over at least 300 ms, (ii) binding reveals linear characteristics, (iii) only the duration of the period of edge element anti-offset matters, (iv) transient aspects related to stimulus onset or offset seem not to play a role, (v) attention is crucial for feature fusion. These results make restrictions on temporal binding mechanisms but are in good accordance with attentional mechanisms underlying feature binding.

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◆ **The binding problem: an investigation using the change blindness paradigm**

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We investigated the nature of the internal representations at 100 ms using a change blindness paradigm. In each trial, two displays were presented sequentially and the task was to say whether the second was different from the first. The first display, containing eight objects that varied on three dimensions—size, shape, and colour—was constant across trials. It remained on the screen for as long as the observer desired. The second display was presented for 100 ms. If observers detected a change in the second display, they indicated which of the eight objects had changed. In experiment 1 ($N = 19$), we compared change to a single object on a single dimension and changes to two objects (each on a different dimension). The two main results were (a) change detection was about 50% for the single-object change and 75% for the two-object/two-dimension change, and (b) performance (both change detection and localisation) for the two-object change trials was well predicted with a probability summation model. In experiment 2, we asked the question whether the representation at 100 ms would be in a bound state. The manipulations were the same as in experiment 1 except that for the two-dimension change, both changes occurred within the same object (and location). Although overall performance was similar to that in experiment 1, the probability summation model overestimated performance. At the same time, performance was better than might be expected from the single-dimension change conditions. These results suggest that by 100 ms object representations have not quite achieved a bound state.

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◆ **The influence of shape discriminability on view-sensitivity**

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Our recognition system is sometimes highly sensitive to the viewpoint from which an object has to be identified, yet in other cases performance is view-invariant. What are the conditions under which this generalisation across view is more or less successful? One proposal is that view-sensitivity increases as the difficulty of shape discrimination increases. We report evidence from a range of studies that discrimination difficulty can both directly and indirectly influence view-sensitivity to plane misorientation and depth rotation. First, direct effects of discriminability

were found in sequential picture-matching studies depicting depth-rotated views of novel, complex, 3-D objects. Shape discrimination on mismatch trials was more view-sensitive when two similar shapes were shown. Second, indirect effects of discriminability were found in similar studies but where discriminability on mismatch trials was manipulated between subjects. Match trials were identical in all mismatch contexts. View-sensitivity increased for match trials which were mixed with mismatch trials presenting more similar shapes. Third, similar indirect context effects of discriminability on view-sensitivity were found for plane-rotated views of familiar objects but these effects were weak and transient. Such effects may be hard to obtain for familiar objects where we have an expectation of the required level of shape discrimination that is difficult to alter. Nevertheless shape discriminability is clearly critical in determining the view-sensitivity of recognition. Varying mismatch trials to depict pairs of shapes which are more or less similar influences view-sensitivity directly and changing the overall context of discrimination difficulty influences view-sensitivity indirectly on identical trials.

◆ **Orientation congruency effect in object recognition**

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There is plenty of evidence that object recognition is orientation-dependent, but there is still considerable debate why recognition performance depends on orientation. It was proposed that recognition relies on an adjustment of a perceptual reference frame [Graf, 2002 *Form, Space and Object. Geometrical Transformations in Object Recognition and Categorization* (Berlin: Wissenschaftlicher Verlag)]—so that the recognition of disoriented objects would be facilitated if it is preceded by a different object in the same orientation. These orientation congruency effects were demonstrated previously for letters (Jolicoeur, 1990 *Journal of Experimental Psychology: Human Perception and Performance* **16** 351–364) and for novel objects (Gauthier and Tarr, 1997 *Perception* **26** 51–73), but not yet for common objects. Two objects from different categories were presented in close temporal contiguity in brief masked displays, either in the same or in different picture plane orientations. Subjects were required to name the objects. The main dependent measure was the number of errors. Line-drawings of twenty-four common objects were employed. Presentation times for the second object were individually adjusted before the test phase such that accuracy was at 80%, when using a different set of objects. Naming accuracy was significantly higher when the orientation of the second object was congruent with the orientation of the previously presented object. Thus, an orientation congruency effect could be demonstrated also with common objects from different basic-level categories. The results suggest that the recognition of disoriented objects involves an adjustment of an abstract frame of reference which facilitates the recognition of different objects in the same orientation. This finding provides further important constraints for any model of object recognition.

◆ **Categorisation performance depends systematically on shape transformations**

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The shape variability of objects from the same basic-level category can be conceptualised by transformations which continuously change object shape. Morphing between members of a basic-level category allows to systematically vary the shape of common objects. We demonstrated that categorisation performance depends on the amount of shape transformation, using a sequential matching task (Graf and Bülthoff, 2003, EuroCogSci, Osnabrück, Germany). We further investigated shape dependence of basic-level categorisation with name matching and rating tasks. We created five category members (1%, 25%, 50%, 75%, and 100% morphs) for twenty-five basic-level categories, based on morphable 3-D object models. Objects were rendered as grey-level images and presented in a canonical orientation. In the speeded name-matching experiment, subjects had to decide whether an object corresponded to a category name. In a second experiment, subjects were required to rate the typicality of the objects, ie they had to rate how well the objects corresponded to their mental image of the category. Both name-matching latencies and typicality ratings depended systematically on the amount of shape transformation. Name-matching latencies were significantly shorter for exemplars that were more in the middle of the morphing sequence. These exemplars were also rated as more typical in experiment 2. The findings confirm the systematic dependence of categorisation performance on the amount of shape transformation. Shapes that are rated as more prototypical are categorised faster. This shape-dependence in basic-level categorisation is reminiscent of the orientation-dependence in recognition, where the canonical perspective is rated as more typical and recognised faster [Palmer et al, 1981, in *Attention and Performance IX* Eds J Long, A Baddeley (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 135–151]. Overall, the results support an extension of the image-based model of recognition (Bülthoff et al, 1995 *Cerebral Cortex* **3** 297–260) to basic-level categorisation.

◆ **Mirror-reflecting and/or rotating a picture of an object: what happens to the shape percept?**

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A two-dimensional picture is inherently ambiguous: the actual layout of the depicted three-dimensional scene is never fully determined. For instance, objects of which the depths are transformed affinely, by depth scaling and/or shearing, possibly generate one and the same picture. When pictures are mirror-reflecting and/or rotated, the set of plausible scenes corresponding with the depicted scene has not changed. Would then the picture ambiguities be solved the same way or differently depending on the manipulation of the picture? In order to find out, we manipulated a set of vertically oriented (V) and a set of horizontally oriented (H) reference pictures in three ways: (Type 1) mirror-reflecting about the picture's long axis; (Type 2) rotating about 180°; (Type 3) rotating about 180° and subsequently mirror-reflecting about the picture's long axis. On the basis of local attitude settings performed by the participants, the pictorial relief was calculated for each picture. In case of (V), the pictorial reliefs were rather similar for Type 1 pictures with respect to the reference pictures; in case of (H), similarities were found between Type 3 and the reference pictures. Both Type 1 pictures for (V) and Type 3 pictures for (H) are in fact left-right mirror-reflecting versions of the reference pictures. All other comparisons between the pictorial reliefs of the other picture types with their reference pictures showed strong dissimilarities that could be completely explained by different solutions to the ambiguities, eg depth scaling and shear.

◆ **Short-term visual and conceptual priming with line drawings of everyday objects**

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To dissociate visual and conceptual components of primed object identification, we manipulated the prime-target relationship in a short-term priming paradigm with five conditions: (i) identical, (ii) same basic level category, (iii) similar outline shape but conceptually unrelated, (4) same superordinate category, and (v) completely different. In conditions (i), (ii), and (iii), priming is visual because the outline shapes are primed. In conditions (i), (ii), and (iv), conceptual priming decreases gradually. All primes and targets were line drawings of everyday objects. Primes were shown for 35 ms following a 400 ms forward mask and followed by a 17 ms backward mask. After a blank interval of 124 ms, the target appeared on the screen with a presentation duration which we adapted to induce 50% correct identification. After another backward mask of 250 ms immediately following the target, subjects typed the name of the target object they thought they saw. In the first experiment, we obtained a significant positive priming effect when comparing conditions (i), (ii), and (iii) with (v). We did not find significant differences between (i), (ii), and (iii), and between (iv) and (v). This pattern of results strongly indicates that priming is mainly driven by the visual similarity of the outline shapes. To dissociate positive priming from conditions (i), (ii), and (iii) from a possible negative interference effect from the control condition itself, we used a large cross as neutral condition in the second experiment. To control for influences of prime identification, subjects had to identify both the prime and the target in a list of seven alternatives in a forced-choice task. Results are discussed in the light of current models of priming, including visual and conceptual components as well as bias and sensitivity parameters. [Supported by the Research Council of the University of Leuven (OT/00/07).]

◆ **Priming between two-dimensional shapes depends on structural correspondences:**

Evidence from perceptual categorisation

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Short-term priming effects between two-dimensional unfamiliar shapes were studied in a categorisation paradigm. The global spatial structure of each of the shapes was defined by three binary-valued dimensions: symmetry (symmetrical/asymmetrical), elongation (elongated/not elongated), and orientation (upright/inverted). Reliable priming effects (in terms of reductions in reaction time) between shapes on consecutive trials were observed as a function of their structural correspondence on the dimensions, and as a function of the category structure manipulated across three experiments. First, facilitations were observed when priming and primed shapes were identical (experiments 1 to 3) or when they corresponded on two dimensions which were correlated in the category structure of each experiment: elongation and orientation (experiment 1), symmetry and orientation (experiment 2), and symmetry and elongation (experiment 3). Second, priming occurred across the three category structures when priming and primed shapes

corresponded on symmetry but not on elongation; no consistent priming effects were observed, however, when the shapes corresponded on elongation but not on symmetry. In general, priming effects occurred between shapes belonging to the same or to different response categories, although priming was reduced in the latter case. Overall, the results provide evidence that perceptual priming between shapes is determined by their structural correspondence on symmetry and orientation, and that these attributes are encoded in representations mediating shape perception. The priming effects are also discussed in the context of exemplar-based models of perceptual categorisation.

◆ **Interactions between object properties under view changes: Local versus global effects**

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View changes can affect object recognition in different ways depending on the object properties used (eg colour is relatively invariant). Instead of trying to explain recognition by specific properties, we focused on effects of different kinds of properties on object recognition under view changes. We used bent tube-like objects and the properties we used were overall curvature, angle between the upper and lower part, and width of the tube. An object has different properties, whose interactions are important when the object is shown under different views. The simplest kind of interaction might be addition where discriminability of one property (eg width) is added to that of another property (eg curvature). Width, being less view-dependent, might veto angle, regardless of the latter's discriminability. As a final example, curvature might signal the view adequately so that angle can be employed more efficiently. By using small differences between properties, views, and their combination in same-different tasks, we represented the stimuli in a multi-dimensional space. This served as a calibration for low-level effects. The results were compared with a matching task where property and view had to be matched between two stimuli. Our main goal was to investigate the interactions between different properties on object recognition in a more 'global' task with more dramatic view changes. For this, we first tested performance for single properties. We discuss the results of the experiments where properties are combined in terms of the previously noted interactions. Finally, a variant of the matching task in which the view was fixed and only the properties were adjustable, allowed us to look at the absolute estimates of the properties under view changes.

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◆ **Object-internal structure modulates object-based inhibition-of-return**

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Vecera et al (2000 *Perception & Psychophysics* **63** 308–321) have recently shown, using divided-attention tasks, that targets are detected more accurately when they occur on the same structural part of an object than when they occur on different parts. This suggests that attention can be directed towards object's internal features. We present converging evidence using an implicit measure of selection based on the object-based inhibition-of-return (IOR) paradigm with 2-D and 3-D object displays. The results show that IOR is attenuated when cues and targets appear on the same part of an object, relative to when they are separated by a part boundary. These findings suggest that object-based mechanisms of selection can operate over shape representations that make explicit information about object's internal structure.

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◆ **Segmentation of object outlines into parts: A scale – space analysis**

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We have a large data set of 88 outlines of everyday objects segmented by two hundred subjects. In previous research (De Winter and Wagemans, 2001 *Journal of Vision* **1** 421a), we have analysed these normative segmentation data to investigate the role of local properties of the contour curvature and global shape properties at the level of the original contour drawing. In the present study, we re-examined these data at different spatial scales of contour smoothing [Witkin, 1986, in *From Pixels to Predicates: Recent Advances in Computational Vision* Ed. A Pentland (Norwood, NJ: Ablex) pp 5–19]. In a first analysis, we tested the hypothesis that curvature singularities are more popular as segmentation points if they survive longer at larger spatial scales (ie the 'scale' of the singularity). The correlation between segmentation frequency and scale is positive ($r = 0.35$) for negative minima (m–), negative ($r = -0.20$) for positive maxima (M+), and virtually zero ($r = 0.05$) for inflections. Thus, stronger negative minima are indeed more attractive as segmentation points, while the opposite holds for positive maxima. In a second analysis, we examined

the nature of the contour segments of the resulting parts. We first determined the most popular part cuts and then described the curvature properties of the corresponding shortest contour segment. We then determined the spatial scale of the part cut (as the highest of the spatial scales of the two segmentation points) and the maximal smoothing scale of the overall shape (before becoming completely convex). In about 30% of the cases, the resulting contour segments consist of $m-$, $M+$, $m-$ strings at one of these two spatial scales. These data thus support previously proposed segmentation models, while leaving many other factors unexplained that we incorporate in a more integrated theoretical framework.

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◆ **The role of visual synchrony in perceptual grouping revisited**

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Recent psychophysical studies demonstrated that temporal structure can be used by the visual system for perceptual grouping. Positive findings may reflect a grouping mechanism that exploits temporal correlations among neurons encoding local features. However, this mechanism may be critically dependent on stimulus transients. Moreover, temporal grouping may merely reflect the ability to use the information within single stimulus frames. To address the latter account (i) we compared the threshold dependence on duration of flicker detection and grouping, and (ii) we measured grouping performance at contrasts/frequencies at which flicker detection was at chance. Stimuli were grids of achromatic equidistant oscillating dots. In the grouping task, either alternate rows or columns of dots were presented out of temporal phase. In the flicker task, either all the dots flickered in phase or were not modulated over time. Flicker thresholds decreased with stimulus duration, whereas grouping thresholds did not change or even increased, pointing to different underlying mechanisms. Moreover, rows and columns were discriminable even when flicker was undetectable. Accordingly, the grouping mechanism has a higher temporal sensitivity than flicker detection. Temporal grouping is therefore unlikely to be based on the ability to isolate information within single frames. In order to estimate the impact of the stimulus onsets and offsets, performance in the grouping task was then measured while stimuli were (a) pre-masked and post-masked, and (b) luminance-ramped. Performance dropped substantially for both masking and ramping, but remained significantly above chance. Thus, stimulus transients are a major, but not the only factor in temporal grouping.

◆ **The structure of object-shape representations in visual recognition**

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A fundamental issue in understanding visual object recognition concerns the structure of 3-D object-shape representations. In this study, we examine two contrasting hypotheses about the primitives of 3-D shape representation based on (i) surfaces (eg Leek and Arguin, 2000 "Surface-based descriptions in object recognition", talk given at the 41st Annual Meeting of the Psychonomic Society, New Orleans, USA; Pentland, 1989 *Spatial Vision* 4 165–182) and (ii) volumetric component parts (eg Biederman, 1987 *Psychological Review* 94 115–147). Converging evidence from two paradigms—part-whole matching and short-term repetition priming—suggests that volumetric components (eg geons) have no special status in 3-D shape representations. The results are interpreted in terms of a surface-based model of 3-D shape recognition.

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◆ **Holistic viewing in visual search**

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According to reverse hierarchy theory (Hochstein and Ahissar, 2002 *Neuron* 36 791–804), holistic, high-level cortical mechanisms are responsible for pop-out—rapid detection of an element that differs greatly from surrounding elements in a single dimension such as colour or orientation. With large-receptive-field attention spread across the entire scene or array, subjects detect presence or absence of targets with response times that are independent of the number of distractor elements. We now study the speed and accuracy of detecting two 'pop-out' elements simultaneously. Subjects viewed a briefly presented 8×8 array of pink lines oriented at 55° (or 60°) followed by

a masking stimulus after a variable stimulus-to-mask onset asynchrony. On some trials, one or two of the elements were replaced by a pale green line of the same orientation, a pink line of orientation 35° – 40° (or 30°), or a line with both these changes. Subjects reported the number of odd lines, and their nature. Surprisingly, we found that subjects were more accurate at detecting and identifying two targets than single targets—for all types of odd elements. In addition, it was easier to report presence of two odd elements (one with an odd colour and one with an odd orientation) than to report the presence of one odd element that differed from the distractors both in colour and orientation. These results suggest that oddity is detected as a single whole so that arrays with a pair of targets are perceived as distinct unitary structures. The interdependence of detection of two pop-out elements supports the reverse hierarchy theory notion that pop-out depends on high-level large receptive fields.

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◆ **The time course of orthographic and phonological activation in the recognition of Chinese characters**

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We adopted two paradigms using the same target stimuli to provide convergent evidence for the relative time course of the orthographic and phonological activation of Chinese characters. In the repetition-blindness (RB) paradigm (Kanwisher, 1987 *Cognition* 27 117–143), three characters and four symbols were shown in RSVP and the participants were asked to write down the characters. In the primed-matching paradigm (Kimchi, 1998 *Journal of Experimental Psychology: Human Perception and Performance* 24 1105–1118), a prime character was presented first, followed by two target characters after different SOAs, and the participants judged whether the targets were the same or different. The relationship between the two critical characters was manipulated as: (i) with repeated versus unrepeatable components, (ii) valid versus invalid cuing of the phonetic component to the pronunciation of the character, and (iii) homophone versus non-homophone. RB was found for both homophones and sub-character components. Results from primed matching indicated an early and lasting representation of orthography of the component, and a weaker and later representation of phonology of both the phonetic component and the whole character. Taken together, these results suggest a dominant role of the orthography of component, along with a weaker functional role of the phonetic component to cue the pronunciation of the whole character in the recognition of Chinese characters.

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◆ **ERPs of masked primed letter perception in a sparse delayed letter recalling task**

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In an event-related potential (ERP) experiment testing fourteen participants, letter targets were preceded by a briefly presented masked letter prime. Name and case consistency were manipulated across primes and targets so that the prime letter was either nominally identical to the target letter or not, and presented in the same case as the target or not. The results showed that the manipulation of the relationship between prime and target letters had an effect on ERPs generated by letter processing at various latency ranges. The results are consistent with an account of letter perception based on visual form information (case-specific feature detection) beginning around 90 ms after stimulus onset, and that is independent of a more abstract processing operating about 240 ms after stimulus onset. The results are discussed in relation to earlier behavioural studies in which the masked prime paradigm was used, and interpreted within the framework of an interactive activation model of letter perception.

◆ **Visual control of hand movements under modified visual perspectives**

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Hand movements which require a high degree of precision are usually carried out under closed-loop conditions. However, the natural link between motor movements and visual perception is modified as a consequence of employing technical systems such as endoscopic cameras, or resulting from medical conditions, or when using glasses. Performance of motor movements may deteriorate, systematic errors may occur, and adaptation to the new situation may take place.

The development of technical systems should be informed by relevant empirical research. Two experiments were carried out with the aim of investigating the effects of rotations of the visual field on two types of hand movements. The camera was positioned vertically above the participant's working area and could be rotated around the viewing axis (randomised blocks for 0°, 90°, 180°, 270°). In experiment 1, twenty-four participants carried out ballistic pointing movements towards six target points in a randomised design. A significant and systematic directional error towards the pictorial target point was observed. In experiment 2, thirty participants were asked to track three systematically varied stationary patterns with a pen. For rotated-camera perspectives, participants took much longer and produced many more errors. Performance was slightly better for 180° compared to 90° and 270°. While the pointing task is only slightly affected by the rotated-camera perspective, the tracking task suffered severely (five-fold increase of errors). It is interesting to observe that, despite the closed-loop conditions, different hand-movement tasks can be affected to very different degrees by a rotated-camera perspective.

◆ **Incomplete figure perception—the problem of ‘invisible’ masking**

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Our previous findings (2002 *Perception* 31 Supplement, 116) suggested that the Gollin test of incomplete figure perception (Foreman and Hemmings, 1987 *Perception* 16 543–548) and the Mooney test of incomplete silhouette faces may be considered as signal masking problems, in this sense similar to the Poppelreuter test of contour figure extraction from noisy overlapping figures. We considered the incompleteness of a Gollin figure to be the result of its masking by multiplicative noise similar to the texture of transparent windows and opaque elements. The brightness and colour of the opaque elements are identical to the background and size of transparent windows corresponding with the size of fragments of the incomplete figure. In other words, incomplete figures are figures occluded by an ‘invisible’ mask. The purpose of this work has been to determine the statistical properties of the ‘invisible’ mask and to show their connection with thresholds of incompleteness of figures at recognition. We have made additional investigations, which show that the incompleteness thresholds depend on the level of similarity of the spatial-frequency bands of the figure and the ‘invisible’ mask. The thresholds are reduced when the ‘invisible’ mask changes to a visible one. We presented in psychophysical experiments incomplete figures with two sizes, covering the foveal or macular areas. We measured the thresholds of recognition of incomplete figures in normal participants and in neurological patients with ‘filtration agnosia’ and showed recognition-threshold differences for the different tests. This difference depends on the similarity between the spatial-frequency spectra of the visible (Poppelreuter) and ‘invisible’ (Gollin, Mooney) masks with those of the incomplete figure, and also with the localisation of visual system damage.

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◆ **Perceptual completion of image fragments**

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The process of selective integration of spatially separated fragments is central to many visual completion phenomena that are likely to be limited in what sorts of spatial and temporal gaps they can bridge. The three main phenomena investigated here are modal completion, amodal completion, and perceptual closure. Claims regarding the similarity between the underlying mechanisms mediating these forms of completion are assessed by measuring shape-discrimination performance in configurations where the physical gaps present in partly closed and illusory contour configurations have been replaced by a visible occluding surface over the gap. Shape-discrimination latency was measured as a function of contrast magnitude, contrast polarity, and the spatial separation between disjointed elements. Results show that both illusory-contour formation and perceptual closure were affected by variations in contrast polarity positioned at corners in the inducing configuration but unaffected by variations in contrast polarity of collinear segments even at large spatial separations. Results also show an interesting difference between amodal completion and both illusory-contour formation and perceptual closure in that amodal completion proved to be sensitive to variations in the contrast polarity of collinear contour segments. This result implies that grouping of collinear but spatially separated contour fragments over a physical gap in an image is different from the grouping of such segments behind a visible occluder.

◆ The perception of social and mechanical causality

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We report two studies on perceived mechanical and social causality in schematic motion events. Michotte [1963 *The Perception of Causality* (London: Methuen)] claimed that we perceive cause-and-effect, without reasoning/learning, even in displays of two-dimensional moving shapes. This controversial claim was resurrected by recent work on perceptual causality in preverbal infants. Our studies extend existing work with adults from perception of mechanical to social causality [Kanizsa and Vicario, 1968 *Experimental Research on Perception* (Trieste: University of Trieste)]. Also, they directly compare structured ratings of causality and spontaneous reports. Forty-eight (study I) and seventy-two (study II) observers saw 8 or 12 different computer animations of shape A moving up to B, which in turn moved away. Animations varied factorially the temporal and spatial relations of the shapes, and whether they moved rigidly or in a nonrigid, animal-like manner. Observers distinguished physical, social, and no causality in their ratings, based on the spatiotemporal configuration and on agent motion. We found high proportions of physical and social reports to causal, but not noncausal control stimuli. The perception of social causality was somewhat weaker than of physical causality. Most importantly, spontaneous reports showed the same pattern of variation as ratings. Our studies demonstrate perceptual illusions of both mechanical and social causality. The correspondence of ratings and reports argues against two criticisms typical in this area: that ratings distort spontaneous perception because instructions introduce biases, while reports without specific direction are insensitive, because observers may fail to express important detail. The good fit of our measures validates much recent work in this area.

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AMBIGUOUS PERCEPTION, ILLUSIONS, AND ART

◆ A two-tiered hierarchy for perceptual change

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The Necker cube (NC) figure appears to switch between two 3-D perceptual alternatives, 'cube up' (CU) and 'cube down' (CD). However, experienced observers not only report CU and CD but also a myriad of 2-D percepts. Four experienced observers recorded perceptual changes that occurred during observation periods lasting 5 min. In one period they recorded when the CU percept began and finished, thereby giving the number and duration of CU percepts; this was repeated for CD and 2-D percepts. The sum of the durations for the percept of CU was about the same as that for CD; taken together CU and CD percepts accounted for between a third and a half of an observation period. The sum of the 2-D percepts accounted for between a half and two-thirds of an observation period. The distributions of CU and CD percept durations were similar and were modelled adequately by gamma distributions. These percepts tended to be brief (about 1 s) compared to the far more stable, and normally distributed, 2-D percepts. The difference between the characteristics of CU/CD and 2-D percepts is consistent with a system that operates at at least two different tiers of perceptual change. At one level, changes can occur between 2-D and 3-D interpretations. Further changes can occur within either the 3-D or 2-D interpretations, such that if a 3-D interpretation has been accepted then there can be further changes between CU and CD at this subordinate level. Most models of perceptual change only consider this subordinate level.

◆ Effects of top – bottom polarity and figure – ground coding in figural search

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We report data from a discrimination task in which participants were set to search for a target in a display with ambiguous figure–ground organisation (figural search). We show that search was easier when stimuli with a top–bottom polarity were placed in an 'upright' orientation (wide base, narrow top), relative to when the top–bottom polarity was inversed. The effect was magnified with ambiguous relative to unambiguous figure–ground organisation, and it occurred even when participants were set to use colour to parse figure from ground. We discuss the utility of the figural-search task for studying figure–ground coding, and the role of an 'upright' bias for coding perceptual figures.

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◆ **Temporal dynamics in bistable perception**

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Bistable perception arises when a stimulus is consistent with at least two interpretations. We are interested here in the temporal dynamics of bistable perception, that is the temporal variations in dominance periods of one percept over another. Our first bistable experiment consisted of a binocular rivalrous stimulus, namely one Gabor grating presented to the left eye and an orthogonal grating presented to the right eye. The contrast ratio of the gratings was manipulated to affect the mean duration of one or the other percept. The stimulus was presented continuously for periods of at least 2 min and observers were asked to report their percept every time that an auditory signal was presented. The sounds were presented every 2 s with a small temporal jitter to avoid anticipatory effects. Perceptual judgments were averaged over thirty periods. The results show a correlation between the very first percept and the long-term average of the dominant percept. This result indicates that the mechanism responsible for the alternation of percepts is also sensitive to the stimulus properties that drive the first percept. We discuss the implication of our results for the interaction between bottom-up and top-down processing in bistable perception.

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◆ **Binocular rivalry and perceptual stability**

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Binocular rivalry has alternatively been argued to involve rivalry between eyes and/or between stimulus representations. We present a novel method to quantify the relative contributions of eye and stimulus rivalry. Our results suggest that awareness in visual bistability recruits mechanisms that are not engaged in the perception of stable stimuli, leading us to question to what extent findings from rivalrous viewing can be generalised to normal vision. When the presentation of rivalrous stimuli is interrupted by a blank screen, the percept tends to be the same after the interruption as before (Leopold et al, 2002 *Nature Neuroscience* 5 605–609). We presented subjects with a pair of gratings of opposite colour and orientation for 1 s, followed by a 3 s interruption. During the interruption, we swapped either the colour, orientation, or eye of presentation of the gratings. Comparing the percepts reported before and after the interruption allowed us to establish what aspects of perception remained stable. The primary determinant of awareness was the eye in which the stimulus was presented (stable in 74% of trials). Stimulus colour also had a significant effect (stable in 63% of trials). When eye rivalry was abolished by rapidly swapping the stimuli between eyes, the primary determinant of awareness was stimulus colour (stable in 86% of trials). These results clearly demonstrate both eye and stimulus rivalry. Presentation of similar non-rivalrous stimuli for 1 s during the interruption had little effect on the pattern of results. The presence of a given attribute in the non-rivalrous stimulus tended to reduce the probability of that attribute being perceived in the subsequent rivalrous presentation. This effect was weaker than and in the opposite direction to that described above. This pattern of results suggests that awareness in binocular rivalry is mediated by mechanisms only weakly affected by non-rivalrous vision.

◆ **Hysteresis and bistability in a 'Breathing illusion' display**

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We studied the synergetic effects of expanding and shrinking squares occluding a counterclockwise rotating ellipse (eccentricity = 0.85) by means of an animation movie where an ascending (ie expanding squares, ES) and a descending (ie shrinking squares, SS) series were repeatedly presented to subjects. Five subjects had to press a key whenever they perceived a switch from the rigid object to an oozing cross (ES) and vice versa (SS). For each frame of the movie, rates of oozing-cross perception were obtained and a modified psychometric function [Chiorri, 2002 *Metodologia per la Ricerca Sinergetica in Psicologia* (Firenze: CUSL)] was fitted to data. Threshold values for ES and SS were calculated by differentiation, showing negligible differences with respect to those obtained through the classical method of limits. The presence of hysteresis was then statistically demonstrated. Results are explained in terms of minimum principle and amodal completion theory and the ratio between visible and occluded areas of the ellipse proves to be a control parameter for the switching behaviour. Two of the subjects were successively tested in five stationary-squares conditions (−3 standard deviation from ES threshold, ES threshold, general threshold, SS threshold, +3 standard deviation from SS threshold, randomly ordered) and relative strengths (as in Ditzinger et al, 1997 *Biological Cybernetics* 77 23–30) of the alternating percepts were calculated and plotted against experimental time. Contrary to expectations, the oozing-cross

percept was stronger than the rigid object one in the first condition with reference to the last, while percepts showed similar strengths in the range of hysteresis marked by the second and the fourth condition.

◆ **Expansive micropsia**

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Elements in an optic flow field increase in angular size as the field expands with forward motion. If the element size is held constant, there is a resulting illusion of the elements shrinking in size with field expansion. Macpherson (1993 *Perception* **22** Supplement, 121) referred to this as 'expansive micropsia'. The origin of this phenomenon is unclear, but one possible explanation is that it is a result of size-constancy scaling. We have tested the size-constancy explanation by estimating the magnitude of the illusion for a range of stimulus configurations representing candidates for both plausible and implausible flow fields. The results indicate that the magnitude of the illusion is affected significantly by absolute size, being larger for small square elements ($0.5 \text{ deg} \times 0.5 \text{ deg}$) than for larger ($1.5 \text{ deg} \times 1.5 \text{ deg}$) ones. Further, there is a marked ceiling effect with the extent of the field expansion. Finally, the size-shift illusion with line targets is as large when there is an instantaneous displacement accompanied by a random rotation ('implausible') as when the temporal sequence represents a 'plausible' target expansion. We conclude that size constancy does not provide a comprehensive account of the illusory size contraction, and advance an alternative hypothesis based on the M-scaling of size-sensitive detectors with eccentricity.

◆ **Right-angle judgment combined with distortions on perceived length**

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The reported psychophysical experiments were intended to test whether or not length illusions affect right-angle perceptual judgments. A pair of inward or outward wings of the Müller-Lyer figure, or the interval of the Oppel–Kundt figure filled with dots were used as inducing stimuli. A probe dot was placed at an arbitrary point on a virtual axis bisecting the segments defined by each of these configurations. The whole display was presented under monocular vision. By pressing one of two keys on the keyboard, subjects moved the probe dot along the bisecting axis so as to place it at the crossing point of the two imaginary orthogonal lines drawn from the vertices of the wings of the Müller-Lyer figure, or from the ends of the filled interval of the Oppel–Kundt figure. The estimated crossing points were too close to the axis of the inducers (obtuse angle) for the inward-wings, and too far from the inducer (acute angle) for the outward-wings and for the Oppel–Kundt configuration. The angle estimation errors covaried with the illusion strength as it was manipulated by parametrically changing the length and the angle of the Müller-Lyer wings or the number of dots in the Oppel–Kundt figure. The results are interpreted in terms of a 'multi-local' neural mechanism for angle estimation (Heeley et al, 1996 *Vision Research* **36** 3607–3627).

◆ **Illusion of angularity in non-apparent rest conditions**

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When a black-outlined circle on a white background partially occludes an arrangement of black radial stripes on its centre, it is perceived as a smoothed polygon. This is the illusion of angularity (Pinna, 1991 *Perception* **20** 207–218). We suggest a two-stage model accounting for the nonliteral computation of edges involved in this phenomenon. In the first stage, the circle outline is locally distorted and tilted towards the black stripes (Roncato, 2000 *Perception & Psychophysics* **62** 762–785). In the second stage, in order to integrate the local distortions into a global percept, the shape of the outlined circle is approximated to that of a smoothed polygon. This model predicts that the strength of angularity depends on the width, length, and luminance of the inducing stripes. Consider 8 equal inducing stripes (having the shape of sectors of a circle) and make them rotate around their converging point coinciding with the centre of an included and overlapped circle. Owing to the illusion of angularity, the circle is perceived as rotating together with the inducing stripes, despite its constant curvature. The strength of the illusion of angularity was measured through the illusory rotation (or rest) of the outlined circle. Sixty observers adjusted the width of the outlined circle till it reached apparent rest (Metelli, 1940 *Rivista di Psicologia* **36** 319–370). The strength of angularity (i) follows an inverted-U shaped function of the stripes, (ii) increases with increasing length of inducers, and (iii) decreases with decreasing luminance of the circle outline with respect to that of the stripes. These results are consistent with our model.

◆ **Apparent size shrinkage of disparity-defined cylinders**

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When the texture gradient or luminance gradient is used as a depth cue, the perceived width of a vertical cylinder (or the height of a horizontal cylinder) is negatively correlated to its perceived depth (Miura and Taya, 2001 *Perception* **30** Supplement, 22–23). For example, when the widths of a vertical cylinder and a flat square are physically equal, the former appears narrower than the latter. This type of size illusion cannot be explained by conventional models of spatial vision (eg size–distance invariance hypothesis), and suggests that there might be an undiscovered link between perceived size and perceived depth (or 3-D shape). However, it is possible that this illusion stems from monocular features (eg spatial frequency or brightness) and is not related to perceived depth. Here, we examined whether this illusion would occur when stimuli were binocularly defined and had no monocular information. Nine horizontally oriented semicylinders were presented in a stereoscope. They had three different height and disparity curvatures. The observers' task was to estimate the height and the depth of the stimuli by the method of adjustment. Zero-disparity stimuli were also presented to establish the baseline for height estimation. The magnitude of the illusion was obtained by subtracting the baseline height from the estimated one. Results showed that the perceived height decreased as the perceived depth increased. The findings are consistent with studies on monocular stimuli, and suggest that this type of illusion depends on the perceived depth (or 3-D shape). We discuss our findings in the light of a hypothesis assuming a mechanism shared between size perception and depth perception.

◆ **The reverse-perspective illusion is not caused by binocular disparity**

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Reverse perspective (RP) is an illusion of movement in a static 3-D picture. The effect is seen most strikingly in the artwork of Patrick Hughes and the related 'hollow-mask illusion', and is produced by contradictory (bottom–up versus top–down) information concerning the depth of the objects in the scene. Unlike most other visual illusions, the RP illusion is not experienced simply as 'cognitive dissonance' between the contradictory information-processing, but instead leads to the projection of the contradiction onto the external object itself, such that the object takes on unreal, 'magical' movement of its own. Experiments with prism goggles (Cook et al, 2002 *Perception* **31** 1147–1151) indicated that this contradiction is the cause of the illusion because the illusion disappears during head movement in the direction for which prism goggles reverse the visual field (left/right or up/down), while leaving the illusion intact in the direction unaffected by the goggles (up/down or left/right). In order to eliminate the possibility that binocular disparity plays a role in the illusion, we have built a new type of goggles (using both prisms and mirrors) that do not reverse the visual field, but do reverse the binocular disparity. In an experiment with the goggles, all twenty-five subjects judged the more distant of two objects as nearer (for most of the seven stimuli), thus demonstrating that binocular disparity was a key factor in judging distance (at ~40 cm). In contrast, when viewing (at ~40 cm) 3-D objects built in RP or normal perspective, the illusion was consistently experienced with the RP object and not experienced with the normal perspective object with or without the goggles, thus demonstrating the irrelevance of binocular disparity. Our poster allows viewers to experience this effect.

◆ **Flash-lag without change in feature space is alive and well at late intervals after stream onset**

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A target presented within the RSVP stream of spatially and featurally unchanging items is perceived to appear before its simultaneous replica that is flashed as a single stimulus outside the stream (Bachmann and Pöder, 2001 *Vision Research* **41** 1103–1106). However, the streams that were used to demonstrate flash-lag effect (FLE) with no change in feature space were presented for durations no longer than the typical intervals with which stimulus-driven attention is captured and optimised (eg 150–250 ms). It is therefore possible that perceptual precedence of the in-stream target was an artifact of focusing of attention, maximised at 150–200 ms. To test whether this may be the case, we varied the durations of streams more extensively. We found that FLE for the isolated replica of the target is maximised (up to the value of 70–80 ms) after 130–150 ms

have passed from the stream onset, decreases thereafter; however it is persistent (with values in the range 25–35 ms) at all subsequent epochs of the stream, including the intervals that are typical for inhibition of return and attentional blink and extending beyond 400–800 ms. FLE cannot be reduced to the effect of transient attention.

◆ **Comparing distortions induced by luminance gradients**

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An illusory display is presented in which a luminance gradient moves through the visual field. In front of this moving gradient, a grid of outlined, filled, squares is positioned. The movement of the gradient induces an illusory ‘wavelike’ motion of the superimposed squares, depending on the grey values of the squares and their borders. This effect of the moving gradient was decomposed into a dynamic part and a static part. The dynamic part was investigated by means of an experiment in which a temporal gradient induced a forward/backward pulsing of a single outlined square. The static distortions were investigated by means of two experiments. In the first one, an outlined square was positioned on a (stationary) spatial gradient, which caused the squares to look like trapezoid shapes. In the second one, the outlined squares were positioned on different luminance fields, which affected the apparent size of the squares. In all experiments the same ranges of luminance values for both the inner surface of the square and its borders were orthogonally combined. In addition, displays were also created in which the gradient was inside the square and the luminances of the outside surface and the contour were orthogonally combined. For each of the displays, observers were asked to indicate the direction and strength of the induced distortions. The overall results show large agreements between the dynamic distortion (forward/backward pulsing) and the aforementioned static distortion (trapezoid-like appearances). In contrast, different tendencies emerged between these distortions and the second static distortion dealing with the apparent size. The results are discussed and related to various phenomena reported in the literature.

◆ **Kanizsa figure detection and discrimination: explicit or implicit?**

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Previous studies suggested that perception of an illusory-contour Kanizsa-type figure may involve a temporal sequence of stages (Reynolds, 1981 *Perception* **10** 107–115; Ringach and Shapley, 1996 *Vision Research* **36** 3037–3050). We were interested in the cortical level of these stages, in reference to reverse hierarchy theory (RHT; Hochstein and Ahissar, 2002 *Neuron* **36** 791–804). We presented subjects with four inducing figures (‘pacmen’), which were arranged as if at the corners of a 60° parallelogram. The openings of the pacmen were aligned in 25% of the trials so as to induce an illusory Kanizsa parallelogram. In 50% of the trials, the openings were unaligned or faced outward. In the remaining 25%, three of the pacmen induced a Kanizsa equilateral triangle. Presentations were brief and backward-masked (with SOAs of 50–200 ms). Subjects reported whether they perceived a Kanizsa figure (detection) and which shape they saw, ‘guessing’ the shape even when it was not explicitly perceived (discrimination). Performance improved with SOA, as expected. Surprisingly, for longer SOAs, even when subjects did not explicitly perceive the figure, they were significantly above chance at guessing which shape had been presented ($d' > 1$), suggesting implicit figure perception. An alternative, that figure discrimination without awareness depends on detection of local features was ruled out by the following control: for triangle-shaped figures, when the fourth inducer faced outward, this local cue was used as a signal of a triangle shape only when the figure was perceived explicitly and for longer SOAs. These findings support the RHT view that associates focused attention to local cues with late explicit processing at low-level cortical areas.

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◆ **End-stopped cue detection for subjective surface reconstruction**

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We previously reported a model to reproduce the Kanizsa illusion based on depth-cue-detection and surface-reconstruction algorithms (Kogo et al, 2002 *Lecture Notes in Computer Science* **2525** 311–321). This model gave correct responses to a wide range of variations of Kanizsa figures, and was unique since (i) it first created a ‘relative’ depth map by double convolution algorithm

with Gaussian-derivative-based filters, (ii) the depth map was then created by applying anisotropic diffusion equations to the relative depth map (3-D reconstruction), and (iii) on the basis of psychophysical studies, the modification of the original input was made by linking the depth map to the 'perceived' brightness of the figure. This model, however, only detected L-junction as a depth cue and, therefore, it could not mimic the perception of occlusions with Kanizsa figures that are constructed from end-stopped (ES) lines. To make the model even more robust, we now implemented the end-stopped filter as an additional depth-cue detector. This was accomplished with a conventional filter: a difference of Gaussian (DOG) filter with the positive portion being cut in half orthogonally to the longitudinal direction. This filter gave sharp responses to ES lines but less or no responses to the junctions, ie when a line ends at an intersection. This signal was added to the border map (the signal from the first convolution) and was fed into the second convolution of the previous model. The model created a strong depth signal in the central area in the various Kanizsa figures with ES lines. The results were compared with psychophysical experiments to determine the parameter settings of the model. These results further support the plausibility of the fundamental design of the model.

◆ Priming a visual illusion

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The perception of an illusory word can be induced by using the technique of rapid serial visual presentation (RSVP). If two consequently presented words share the same string of letters ('CREEP' – 'SHEEP'), a partial repetition blindness is induced, generating a free-floating fragment ('SH'). This fragment is likely to be linked to a second one ('IFT') if both combine to a meaningful word (illusion: 'SHIFT'). The illusory word shares the perceptual quality of 'real' words, and is reported with the same confidence. Using event-related brain potentials (ERPs), we examined whether the illusory word shares the semantic properties of a real word. RSVP streams (10 Hz item⁻¹) containing two meaningful words (W1, W2) and a word fragment (FR) were presented to fourteen subjects. Each trial was preceded by a prime word, was semantically unrelated, or related either to the real word (W2), or the intended illusory word. The probability of naming W2, but not the illusion, was 24% for unrelated, and increased to 42% for related primes. The corresponding probabilities for naming the illusion, but not W2, were 52% and 71%, respectively. A pairwise comparison (unrelated – related) was also applied to extract the ERP correlates of semantic priming. If W2 was named, the effects of priming reflected in a negative-going wave starting at 200 ms, located at frontal leads. A similar negativity characterised the semantic priming effect in the case of a word illusion. However, the onset of the more transient ERP effect was delayed at 500 ms, and it was focused at left-posterior leads. The topographical differences of ERPs indicate that priming of real words facilitates the activation of higher semantic associations, whereas it supports the construction of a visual word form if illusions are triggered.

◆ Eye-movement patterns during stereo-motion-induced blindness

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Bonneh et al (*Nature* 2001 **411** 798–801) demonstrated 'motion-induced blindness' (MIB). When a global moving pattern is superimposed on high-contrast stationary stimuli, the latter disappear and reappear alternately. In a previous study (Wagner 2002 *Perception* Supplement, 42) relations between eye-movement patterns and gaze directions were detected, with subject's reports of display component disappearance during MIB situations. These studies were repeated (binocular eye-movement measures) with stereoscopic MIB displays. The stationary MIB targets and a rotating distractor dot-pattern (two rotation rates) were perceived as superimposed surfaces and dissociated by 6 stereo disparities. MIB was reported with distractor rotating either in front or behind the stationary MIB targets. A dramatic saccade-rate decline during MIB periods was detected. Distractor rotation rate affected MIB periods, saccade rate, and binocular divergence. High distractor rotation rate elicited more accurate binocular divergence to the more distant distractor displays, and a more pronounced saccade rate difference between MIB and No-MIB periods. Results have also revealed effects of time-schedule/eye-movement dependence on target appearance and disappearance (eg target reappearance preceded by specific eye-movement features). Results support the view that attentional mechanisms underlie the MIB phenomena.

◆ **Linking motion-induced blindness to perceptual filling-in**

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‘Motion-induced blindness’ (MIB) and ‘perceptual filling-in’ (PFI) are two phenomena in which, after prolonged viewing, perceptually salient stimuli repeatedly disappear out of view for several seconds. Both phenomena have been shown to be much more complex than simple luminance adaptation. Despite the many similarities between MIB and PFI, two differences suggest that they could nevertheless be unrelated: (i) an area surrounded by background stimuli can be perceived to disappear completely in PFI but not in MIB, and (ii) high-contrast stimuli are perceived to disappear less easily in PFI but, remarkably enough, more easily in MIB. Four experiments were conducted in this study, with comparable MIB and PFI displays, to show that: (a) the extent to which stimuli are perceived to disappear depends on their eccentricity for both MIB and PFI, and (b) contrast manipulations affect MIB and PFI in similar ways, but (c) perceptual grouping of target with background stimuli obscures part of the contrast effect in MIB. We conclude that eccentricity, contrast, and perceptual grouping are critical factors in both MIB and PFI, and that they are most likely caused by the same underlying mechanism.

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◆ **“Real men don’t like pink”: Sex differences in colour preference**

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Anecdotally, colour preferences are markedly sex-specific in children: most girls prefer pink; boys dislike pink and tend to prefer darker colours. Do colour preferences persist in adults? What is the biological basis for sex differences in colour preference, if any? Previous reports give variable evidence for such sex differences (eg McManus et al, 1981 *Perception* **10** 651–666). Here we report results of a pilot study on these questions. Twenty observers (ten of each sex; age range 18–32 years) performed a paired comparison task. On each trial, the observer indicated with a mouse cursor which of two simultaneously displayed colours he/she preferred. Each pair was selected at random from a set varying in hue, saturation, and luminance, and displayed on a calibrated CRT monitor as two $2^\circ \times 3^\circ$ patches centred on a white background. Each pair remained visible until the observer responded, typically for less than 2 s. Averaged over all colour pairs, males preferred higher-saturation lower-luminance colours, while females preferred lower-saturation higher-luminance colours. Hue-preference patterns also differed, at each saturation/luminance combination—on average female preferences peaked for pinks and lilacs, while male preferences dipped in the same region. In cone-contrast space, both male and female preferences peaked in the positive S-contrast region, with female peak preferences shifted toward positive (L–M) contrasts, and male peak preferences shifted toward negative (L–M) contrasts. Both male and female preferences were lowest in the positive (L–M), negative S-contrast quadrant (ie for reddish–yellow colours). Females had, on average, faster response times. The results suggest that sex differences in colour preferences exist in adults, whatever their underlying cause. [YL is supported by a Unilever studentship.]

◆ **Mental images tell us a great deal about ‘how’ we see the world and this information can be used to generate more meaningful 2-D representations of ‘real settings’**

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Certain key artists working from ‘life’ have left a legacy of information in the form of intuitive record, revealing the structure of mental images. They have recorded not just ‘what’ is in the world, but also ‘how’ we see it. From my own observations as an artist and from looking at the work of past masters, I have been able to establish convincing ‘handles’ on the various compositions of visual field that the brain uses to project our visual interpretation of the world. Working with these on the picture plane, it is possible to establish new depth cues for 2-D media and to create new computer-generated 3-D forms that are much closer to our mental projections of real objects. These new ‘form’ and ‘depth’ cues arise as two distinct and independent ‘image types’ or ‘data sets’ are correctly aligned forming a pictorial fixation and a spatially composite picture space. This dual spatial referencing system allows the brain to correctly perceive the 3-D proximity of adjacent objects referenced in the picture. I suggest that this system is also our primary tool for establishing the 3-D relationships between objects in our observations of real settings. These developments set out the fundamentals of a new form of illusionary space and demonstrate that we do not see in perspective! They also provide psychophysicists with a new range of stimuli with which to investigate visual perception and possibly illuminate new angles for our understanding of visual processes.

◆ **3-D paintings on a flat canvas: novel techniques developed by the painters John Jupe and Dorle Wolf and their significance for human stereopsis**

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John Jupe discovered that in the peripheral visual field double images can be perceived even when looking with one eye only. This indicates that V1 additionally receives a somewhat shifted visual afference copy from the retina. In his paintings, Jupe guides the viewer's gaze to a well-focused fixation point close to the image centre and provides peripheral objects with double contours which are not consciously perceived, however, owing to fuzziness caused by cortex magnification. Thus, by simulating kind of normal stereopsis, the genuine 3-D information 'flatness' seems to be suppressed, so that monocular depth cues can take over. Single-cell excitations, which show two subsequent peaks when a single luminous stimulus moves through the visual field (D Perrett, 2002, personal communication), are indicative of a double projection. What might be the purpose of such a visual afference copy? In retinotopic cortex projections, the image is extremely distorted. To determine tiny disparities, it might be appropriate to project afference copies to those sites of the cortex where the similarly distorted information from the other eye is expected to arrive. In her 3-D paintings, Dorle Wolf makes coloured areas float above the canvas by enhancing natural chromostereopsis with ChromaDepth glasses, by which the light is dispersed according to the colours of the rainbow [Wolf, 1999 *der farbe leben* (Münsterschwarzach: Viertürme-Verlag), ISBN 3 00 003388 2; colour to the third (in print)]. Flat paintings thus turn into spatial objects which seem to change during observation, as their positions in depth are revealed only step by step. When lateral borders of homogeneously stained planes which adjoin areas of a different colour indicate different positions in depth, they are often perceived as skew, and so are planes containing continually gliding colours. When reflecting several discrete wavelengths, one plane may lead to the impression of several transparent areas being staggered in depth. As the angle of chromatic aberration of the ChromaDepth glasses is constant, perceived depth is seen to increase with the viewing distance.

◆ **Eye movements in artists and visually naïve subjects: Absence of eye-movement-based memory effect in artists viewing complex scenes**

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Training in the visual arts, particularly painting, involves direct interventions on processes involved in object perception. Higher-order processing, figure/ground perception and perceptual constancy must be suppressed in order to enable the artist to apprehend and make use of the fullest possible range of visual features. In order to assess the effects of increased visual activity, we studied eye-movement patterns in a group of painters and a group of visually untrained subjects viewing pictures of complex scenes designed to attract viewing preferences for either object-related features or colour, form, and composition. Subjects viewed the same 16 pictures in two sessions, one uninstructed and one in which they attempted to remember them. Analysis of the eye-movement recordings showed that the artists spent less time overall viewing object-related features, significantly more time on such features in the second session, while untrained subjects preferred to view object-related features throughout. An interaction of group by saccade frequency showed that the visually untrained subjects demonstrated repetition priming, or the eye-movement-based memory effect, expressed as fewer saccades and longer fixations in the second session, while the artists showed the opposite pattern. Results indicate two relatively separate viewing modes for artists, one object-related and one oriented towards primitive features.

◆ **Perceptual constancy and the representational art**

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Our visual experience is not the same as the optical projection on the retina. We perceive the outside world as an invariant static entity full of enumerable objects through internal processes collectively called perceptual constancy. Perceptual constancy plays an extremely important role for the survival of an organism. However, I would like to make the argument that, when it comes to pictorial representation, perceptual constancy poses many kinds of challenging problems for artists of all times around the world, and shapes the outcome of art creations. One of the main effects exerted by perceptual constancy on pictorial arts is the difficulty for the artist to master the principles of linear perspective. Given its power to render a realistic three-dimensional scene on a two-dimensional plane, it is odd that the use of linear perspective has never been spontaneous or even popular outside the Western tradition. Part of the reasons for this curious fact could be attributed to that perceptual constancy, being a cognitive impenetrable nature of our

perception, works directly against the use of linear perspective in pictorial representations. The rules of linear perspective are a set of tricks to reconstruct an accidental projection on the canvas. The work of perceptual constancy, on the other hand, is to erase singularities associated with each object in a given view. I provide examples of children's drawings and non-Western paintings to illustrate the shaping force of perceptual constancy on artistic styles.

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ATTENTION 1

◆ **Attentional modulation of short-range and long-range motion processing**

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It has been proposed that the motion of strip stimulus sequences with interstimulus intervals (ISIs) is mediated by short-range motion processes up to ISIs of around 50 ms and by long-range motion processes thereafter (Scott-Samuel and Georgeson, 1999 *Proceedings of the Royal Society of London, Series B* **266** 2289–2294). We investigated the effect of attention on short-range and long-range motion processing. The stimulus consisted of a central target and four surrounding distractors. The target was a vertical, 1 cycle deg^{-1} sinusoidal grating which was divided into oppositely drifting horizontal strips sampled at 90° phase intervals, with alternate strips having 90° relative phase (the non-aligned stimulus sequence of Scott-Samuel and Georgeson 1999). The adjacent strips moved in opposite directions (left and right) and an ISI of 0–133 ms was introduced between each stimulus frame. The distractors were four vertical 1 cycle deg^{-1} sinusoidal gratings, of which one moved in the opposite direction to the others. Observers were asked to perform three different tasks with the same stimulus display: (i) identify which distractor moved in the opposite direction to the others (distractor task alone); (ii) indicate whether the central strip of the target was moving left or right (direction-discrimination task alone); (iii) perform both tasks together. Observers' performance in distractor and direction-discrimination tasks alone was almost perfect at all ISIs. However, the direction discrimination of the central target was at threshold or below (65%–75% correct) at all ISIs when both tasks were performed together. The result indicates that short-range and long-range motion processing are similarly modulated by attention.

◆ **How much expert observers can benefit from prior knowledge of a target's depth?**

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Several studies have suggested that it is possible to direct attention in 3-D space (Nakayama and Silverman, 1986 *Nature* **320** 264–265). If attention is directed similarly in depth as in 2-D space, it is possible that the prior knowledge of a target's depth plane may not only help to direct spatial attention to a relevant location in space, but also to enhance the sensory quality of the stimulus representations. Our previous results suggest that attention in 3-D space is different from attention in 2-D space, and attending to a particular depth plane helps performance only when vergence eye shifts are possible (Puhakka et al, 2003 *VSS03 Proceedings* 158). To further explore these questions, a new search study was carried out in which two expert observers searched for a digit target among letter distractors. Probability (100%, 50%) of the target locating in a particular depth plane (front, back, no depth), character arrangement between depth planes (8–8, 1–15), and the exposure duration of the search display (40 ms, 50 ms, 100 ms, 150 ms, 200 ms, until response) were varied between blocks. Probability manipulations had a clear effect on performance when the exposure duration was longer than 40 ms. Distributing the characters between the two depth planes enhanced search performance compared to the no-depth condition. Prior knowledge had a clear effect on performance, irrespective of whether vergence shifts were possible or not. Prior knowledge of a target's depth plane can aid search performance even when vergence shifts are not possible, but the result seems to be sensitive to practice effects and quite small changes in experimental conditions.

◆ **Spatial and temporal performance fields: Perceptual and attentional effects**

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Contrast sensitivity and spatial resolution are better and faster along the horizontal than vertical meridian and along the lower than the upper region of the vertical meridian. Whereas covert

attention improves discriminability at all isoecentric locations to a similar degree (Carrasco et al, 2001 *Spatial Vision* **15** 61–75), it accelerates information accrual more at the slower locations, practically eliminating the temporal asymmetry (Carrasco et al, 2002 *Visual Science* **5** p.51). We investigated whether: (a) the spatial and temporal asymmetries are reflected in perceptual stationary (texture and acuity) and dynamic (illusory motion and temporal gap) tasks; (b) covert attention alters these asymmetries in these perceptual tasks. In a 2AFC acuity-discrimination task, observers reported whether a Landolt-square target contained a gap on the right or left side. Performance decreased with eccentricity, more so at the north than south locations, and less so at the east and west locations. Attention improved performance to a similar degree at all isoecentric locations, so that performance asymmetries remained. The same pattern of results was observed in the texture-segmentation task. In a 3AFC illusory-motion discrimination task, observers reported if a line, presented all at once, appeared to be drawn from one or another end or to appear all at once. Observers were less prone to the line motion illusion at the north than at all other locations, but attention practically eliminated the asymmetry. The same pattern of results was observed in the temporal gap task. We conclude that: (i) spatial asymmetries are manifested in static tasks and remain present under covert attention; (ii) temporal asymmetries are manifested in dynamic tasks but are practically eliminated under covert attention.

◆ **Attention and scintillation**

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The scintillation grid is a recently discovered visual illusion, created by superimposing white discs on the intersections of orthogonal gray bars on a black background. Even though the entire display is stationary, observers perceive dark spots appearing and disappearing rapidly within some of the white discs. This scintillation effect is correlated with eye position and eye movements (Böhm et al, 1997 *Perception* **26** Supplement, 27; Schrauf and Wist, 1999 *Perception* **28** Supplement, 122). Here, we investigate whether covert shifts of attention, as revealed by cueing and visual-search paradigms, can also affect the illusion. Subjects indicated which of the nine intersections of a briefly flashed scintillating grid had or had not scintillated. In one condition, a spatial cue was flashed shortly before the grid, drawing exogenous attention to that location. In another condition, subjects engaged in a difficult visual search for a rotated L among rotated Ts: we assumed that, on average, endogenous attention was present at the location of the target on correct, but not on incorrect trials. In both conditions, we find that the chance of a particular intersection scintillating is directly correlated with distance from the attentional focus, regardless of the location of the fixation point. This suggests that the dynamics of this illusion might reflect the distribution of attention in space and time.

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◆ **Attentional effects on adaptation to gratings**

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We studied attentional effects on the adaptation of gratings. Contrast threshold and perceived vertical orientation were assessed before and after exposure to a sequence of adapting gratings (two sinusoidal gratings of 5 cycles deg⁻¹, subtending 4.5 deg, duration 500 ms, ISI 500 ms, centred on a small fixation circle). The subsequent test grating varied either in contrast (contrast threshold) or in orientation (perceived vertical). Attention to adapting gratings was manipulated in five conditions: no task during adapting period (1), same/different discrimination with respect to contrast or orientation of adapting gratings (2–3), ditto with respect to orientation or luminance of fixation circle (4–5). The results show the expected contrast threshold elevation (CTE) and tilt aftereffect (TAE) due to adaptation. With any task during the adapting period (conditions 2–5), CTE but not TAE was significantly larger than with passive viewing (condition 1). We attribute this to the alertness component of attention, which increases activity and consequently enhances adaptation. The differential effect on CTE and TAE is expected because the former reflects absolute and the latter relative sensitivity of orientation-tuned channels (Coltheart, 1971 *Psychological Review* **78** 114–121). Interestingly, attending the fixation circle (conditions 4–5) rather than the adapting gratings (conditions 2–3) decreases TAE significantly, while leaving CTE unchanged, suggesting that selective attention modulates only the former. Our results imply a hierarchy of adaptation mechanisms, with contrast adaptation at a lower (preattentive) level and orientation adaptation at a higher (attentive) level of visual processing.

◆ **The phenomenology of attention in a selective-attention task with distractors**

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In the study of the effect of attention on the phenomenal appearance of objects, Prinzmetal et al (1998 *Journal of Experimental Psychology: Human Perception and Performance* **24** 261–282) claimed that the phenomenal vividness of an attended object resulted from the reduced variability of percepts, not from a representational change. However, we (2001 *Investigative Ophthalmology & Visual Science* **42** Supplement, 865) examined the possibility that the target stimulus in their task was too simple to properly reveal the effect of attention on the perceptual appearance, and, using a selective-attention task with a composite target, we showed that the effect of attention on the perceptual appearance is due to the representational change as well as the response variability. We note that there are two points to be further examined for consolidating this conclusion. One point is task difficulty and the other is related to the task itself. To investigate further into these points, we adopted a conventional selective-attention task with distractors. Subjects were instructed to determine whether the central matrix of letters had contained the letter F or T and at the same time to identify the colour or orientation of the peripheral target among the distractors of desaturated colour or partial line squares, respectively. We found again in this relatively easy and conventional selective-attention task that significant mean shifts occurred for colour and orientation percepts in the diverted-attention condition, which verifies our previous results.

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◆ **Is filtering cost involved in stimulus-driven attentional capture?**

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Folk and Remington (1998 *Journal of Experimental Psychology: Human Perception and Performance* **24** 847–858) differentiated two forms of attentional capture: non-spatial filtering cost and spatial attentional shift, but did not provide direct evidence for the existence of filtering cost. We examined whether filtering cost involved in attentional capture by considering three characteristics of filtering cost: (i) only discrimination, but not detection, yields filtering cost, (ii) foreknowledge does not reduce the cost, and (iii) filtering cost increases with display size (Kahneman et al, 1983 *Journal of Experimental Psychology: Human Perception and Performance* **9** 510–522). In experiments 1 and 2, two kinds of tasks (detection and discrimination) with exactly the same stimuli were used in a modified cuing paradigm. Five levels of SOA (–150, –50, 0, 50, 150 ms) were manipulated, and the participants either had or did not have foreknowledge about the irrelevance of the distractor to the target. Distracting effects were found in discrimination tasks but not in detection tasks, and foreknowledge about the irrelevance of the distractor did not reduce the distracting effects in discrimination tasks. In experiment 3, however, when different numbers of distractors were presented, an effect akin to visual marking was found when the distractor preceded the target (SOA = –500 ms), but no sign of filtering cost was found when the distractor was presented simultaneously with the target. Taken together, the concept of filtering cost does not seem to fully characterise the distracting effect found in attentional capture.

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◆ **Can contingent attentional capture override endogenous orienting to a specific location with 100% validity?**

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Folk et al (2002 *Perception & Psychophysics* **64** 741–753) demonstrated contingent attentional capture even outside the focus of attention, while Yantis and Jonides (1990 *Journal of Experimental Psychology: Human Perception and Performance* **16** 121–134) failed to find stimulus-driven capture by onsets when the target location was precued by a 100%-valid endogenous cue. Folk et al used an RSVP sequence where letter identification was performed to control the focus of attention, and found that peripheral colour distractors produced a decrement in central target identification in matched distractor–target colour condition. We examined (i) whether a salient abrupt onset could capture attention involuntarily in displays similar to those of Folk et al, and (ii) whether contingent capture outside the focus of attention also occurred when focal attention was precued endogenously to a specific location with 100% certainty. Our results showed that no stimulus-driven onset capture occurred in displays similar to those of Folk et al, and that the action of shifting attention to a specific location still produced contingent attentional capture by colour distractors. We conclude that stimulus-driven attentional capture is not strongly automatic because

no onset capture occurs even when focal attention is maintained in fixation, and that attentional control settings are strong enough to override endogenous orienting with 100% validity. [Supported by grant NSC91-2413-H-002-013.]

- ◆ **Effects of explicit versus implicit instructions on visual repetition priming by shape and colour**
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Whether visual repetition priming by shape or colour occurs automatically or requires top–down processing is a debated issue. We investigated effects of shape and colour of primes on the identification of targets as a function of the instructions given. Four independent groups of ten observers were tested. Group 1 had to identify the shape of a target following a prime *and* was explicitly told that the prime preceding the target could be relevant for the task. Group 2 had to identify the colour of a target following a prime *and* was explicitly told that the prime preceding the target could be relevant for the task. Group 3 was given no further instructions than to identify the colour of the second of two successive stimuli. Group 4 was given no further instructions than to identify the shape of the second of two successive stimuli. Primes and targets could be congruent in regard to shape and colour, shape only, colour only, or completely non-congruent. In neutral trials, no prime preceded the target. Different conditions with a constant number of trials were presented in random order. Shape-congruent primes and targets produced significantly shorter response times (RTs) compared with neutral trials in the explicitly instructed group identifying target shape. Colour-congruent primes and targets produced significantly shorter RTs compared with neutral trials in both explicitly and implicitly instructed groups identifying target colour. Shape priming thus requires explicit instructions. Repetition priming by colour does not, occurs automatically, and is explained by spatiotemporal probability summation. Shape priming implies top–down matching (Grossberg, 1999 *Consciousness and Cognition* 8 1–44) of prime–target relationships where top–down expectation signals activated by the prime are matched to bottom–up signals activated by the target.

- ◆ **Does top – down attentional control deactivate inhibition of return? Evidence using temporal order judgments**

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Previous research has shown that inhibition of return (IOR) does not affect temporal order judgments (TOJs). As TOJs have traditionally been used to measure perceptuo-attentional processing, their failure to show IOR has serious implications for a perceptuo-attentional account of IOR. However, studies using other perception-only measures (eg accuracy measures) have shown that IOR can affect performance at this level. These findings pose the interesting question how two measures of perceptuo-attention can provide such contradictory results. In an attempt to resolve this issue, some authors have suggested that observers adopt a top–down control of attentional orienting when performing TOJs, which can cause IOR to be deactivated. If this is true, then this hypothesis suggests that TOJ data might not be useful for drawing conclusions about IOR.

On this poster we report experiments that test the top–down explanation of TOJ in relation to IOR. In the first experiments, observers were required to make either detection or TOJ responses to targets in identical display sequences. Results showed that whilst IOR was observed for detection responses, IOR did not affect TOJs. In a further experiment, observers had to make TOJ judgments in a task designed to disrupt a voluntary allocation of attention. However, the results showed that IOR did not affect TOJs even under these conditions. Taken together, the findings of these experiments do not support the idea that TOJs can be performed by using a top–down allocation of spatial attention.

- ◆ **Attentional biases to stimuli associated with threat reflect difficulty in disengaging attention rather than preattentive identification**

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Recent evidence suggests that individuals show a preattentive bias for threat stimuli (eg Öhman et al, 2001 *Journal of Experimental Psychology: General* 130 466–478). However, these findings may reflect low-level processing of simple features. The first two experiments used a visual-search paradigm in which search could be guided by associations with threat, but not by simple feature differences. Two abstract target stimuli and a set of distractor stimuli were constructed

by rearranging a set of basic shape components. Emotional valence of the target stimuli was manipulated by pairing targets with either negative or neutral pictures. Results from both experiments showed that emotional stimuli were not detected preattentively. In fact, the search slope for negative targets was just as high as that for neutral targets, demonstrating that they produced no attentional advantage. Importantly, data from a conditioning measure indicated that targets were conditioned to carry affective valence. In the third experiment, we investigated whether threat stimuli hold attention more effectively than neutral stimuli. A small photo, either negative or neutral appeared, followed by a target. When the target appeared at a different location from the photo, subjects experienced more difficulty in disengaging from negative than from neutral photos. While we find no evidence for the preattentive detection of conditioned threat stimuli, once a threatening stimulus is attended, disengaging attention from it can be difficult.

◆ **Rapid serial shifts of attention evoked by subliminal primes?**

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There is evidence that attention moves slowly from one attended location to the next (Ward et al, 1996 *Cognitive Psychology* 30 79–109). On the other hand, using an electrophysiological indicator ('N2pc'), Woodman and Luck (1999 *Nature* 400 867–869) showed rapid shifts of attention. This indicator, N2pc, may also be evoked by masked stimuli (Jaskowski et al, 2002 *Psychological Science* 13 48–54; Woodman and Luck, 2003 *Psychological Science* in press) as is an indicator of subliminal motor activation ('LRP'). In the present study we tested whether N2pc and LRP would indicate rapid shifts of attention and motor preparation between a series of two serially presented masked primes followed by the masking main stimulus. Both primes and the main stimulus were pairs of left and right stimuli, with the target figure on one side, requiring a key-press on that side to the main stimulus. Small copies of the target figure were also displayed in the primes. When the target figure was changing its location from one prime to the next, N2pc likewise shifted from one side to the other, in spite of the short (40 ms) SOA between primes. This high-speed shift of attention is in contradiction to claims that attention operates slowly.

◆ **Contextual effect, figure–ground organisation, and attention**

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Performance of detecting a Gabor patch is facilitated when the target Gabor is in a collinear configuration with the flanking Gabors (the contextual effect—Polat and Sagi, 1993 *Vision Research* 33 993–999). We presented to participants a group of aligned Gabors as a diagonal figure pattern and another homogenous group of orthogonally orientated Gabors as a background pattern, inducing a figure–ground percept in the display. Attention was manipulated so that either an area of the figure or that of the background was cued before the presentation of the display. Participants were asked to perform a detection task to the central target Gabor. A larger facilitation effect was found when the target was collinear with the figure than when it was collinear with the background. Precuing the background produced a larger difference in the contextual effect between the figure and the background than precuing the figure. These results suggest that the collinear contextual effect may not be an effect solely due to local inter-stimulus connectivity. Figure–ground organisation and its interaction with attentional control also contribute to the contextual effect.

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◆ **Size assimilation and attention**

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Attentional effects on size assimilation were studied with the use of Delboeuf's concentric-circles figure. Allocation of attention was varied by alternative judgment-order instructions: starting the estimation with either the inner circle as a test or with the outer circle. Absolute and relative diameters of the circles were varied in a consecutive manner (ranging between 12 and 45 mm), and apparent size was judged by the method of magnitude estimation. Induced size depended upon the diameter ratio—maximal assimilation occurred at an inner-to-outer ratio of 0.69 (overestimation of the inner circle) and of 0.51 (underestimation of the outer circle). In addition, size assimilation varied with the absolute diameter difference of circles in a nonlinear way. Allocation of attention had a modulating effect on size induction; specifically the circle judged

initially was estimated more veridically, indicating weaker assimilation. Moreover, an asymmetry of assimilation effects occurred in that the smaller (inner) circle was affected more strongly than the larger (outer) circle. The results suggest that size induction does not depend merely on stimulus variables but also on instruction-modulated allocation of attention which might itself essentially rely on differential figure–ground assignment: the attended test circle, perceptually emerging as the figure, is more resistant to the inducing context; hence its perceived size remains more veridical. Conversely, the induction of the initially attended circle appears to be stronger on the subsequently attended circle that has ground character and is thus more prone to size distortion.

◆ **Global feature-based attentional effects provide evidence for visual binding outside the locus of attention**

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Attention to a stimulus feature can influence neural responses to this feature outside the locus of attention. We studied whether this global feature-based attentional modulation can also have an effect on the task-irrelevant features of ignored objects that share the attended feature. We measured the modulation of motion aftereffect (MAE) by global feature-based attention. The adapting stimulus consisted of two apertures of moving dots, one on the left and one on the right side of fixation. The attended aperture contained randomly moving dots (50% red and 50% green). In the ignored aperture, 70% of dots, ‘effectors’, were moving upward, while the rest of them, ‘distractors’, alternated direction every 4 s between leftward and rightward. These two groups of dots were also coloured differently. During adaptation, observers attended either to the red or green randomly moving dots and performed a luminance-increase detection task. MAE duration was measured in the ignored aperture. We found that the MAE was significantly longer when the attended colour and the colour of the effectors in the ignored aperture were the same, compared to when they were different. This difference in the MAE durations increased as the luminance-increase detection task became more difficult. These results provide psychophysical evidence that global feature-based attentional modulation is propagated to the task-irrelevant features of the distant, ignored object that shares the attended feature. The spreading of attentional effects across attributes found in the present study (colour to motion) implies that surface-based feature binding occurs outside the locus of attention.

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◆ **Scene-based and object-centred facilitation: Evidence for attention at multiple levels of spatial description**

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Previous studies have suggested that attention can operate at two levels of spatial description: scene-based and object-centred (eg Tipper et al, 1999 *Perception & Psychophysics* **61** 50–60). Here, we investigate the possibility that facilitation at the egocentric and allocentric coordinates of an endogenously cued object (Barrett et al, 2003 *Perception* **32** 41–52) reflects these separate levels of spatial description by manipulating the way that objects in the display are grouped. Drawing upon evidence that attention differentially activates grouped and ungrouped objects (eg Fox, 1998 *Perception & Psychophysics* **60** 1004–1021), pictorial cues were used to influence the formation of a perceptual group in three conditions: (i) unjoined, (ii) joined, and (iii) enclosed objects. The data revealed no main effect of grouping, although a small effect of grouping was observed at the cued egocentric coordinate. An advantage in moving attention from the cued egocentric location in grouped compared to ungrouped displays was also observed. The results are interpreted within a multi-coordinate frame model in which priming at the egocentric location reflects the activation of an object localised in scene-based coordinates and priming at the allocentric coordinate reflects the activation of an object’s components within an object-centred frame of representation.

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◆ **The measurement of the salience of targets and distractors through competitive novelty**

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Salience is normally strongest in a region if small neighbourhoods in that region are dissimilar from neighbourhoods elsewhere in the image. Measures based on this principle have been used for image compression (Stentiford, 2001, 22nd Picture Coding Symposium, April) and assessing cell damage (Stentiford, 2002 *Proceedings of the SPIE—The International Society for Optical Engineering* **4662** 244–253). This paper reports results of experiments using images of targets and distractors [Sobel and Cave, 2002 *Journal of Experimental Psychology: Human Perception and Performance* **28** 1055–1070; Wolfe et al, 2002 *Vision Research* **42** 2985–3004; Wolfe, 1998, in *Attention* Ed. H Pashler (Hove, UK: Psychology Press); website: www.ee.ucl.ac.uk/~fstentif/] in which the roles of colour, orientation and scale are explored. It is found that the edges of objects and line ends attract high measures of attention unless those edges and line ends themselves predominate in the image. Distractors that obtain higher measures of attention normally correspond to those cases in which targets are harder to find. For example, the higher measures of attention are generated by distractors when they are different. When orientation differences are small, the neighbourhoods must be of a sufficient size to encompass features that discriminate between target and distractors. This draws a parallel with the finding that smaller-group search is encouraged by densely packed arrays (Sobel and Cave, 2002 *Journal of Experimental Psychology: Human Perception and Performance* **28** 1055–1070).

◆ **Attention-induced blindness to disparity change**

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We have previously reported a paradigm in which selective attention could be modulated in temporal domain by using two synchronised rapid serial visual presentation (RSVP) streams (features: colour and motion). A switch between the streams evoked a transient deficit in visual motion perception (Sahraie et al, 2001 *Vision Research* **41** 1613–1617). Here we report on how disparity-defined depth can also be modulated by attention by using a similar paradigm. Ten subjects viewed a local stream, defined by a fixation point changing colour every 100 ms. A red fixation provided a 'cue' to switch attention to a global stream. The global stream consisted of static black/white random noise with an annulus surrounding the fixation appearing in a different depth plane (baseline plane) with respect to the background. Subjects' task was to detect a transient disparity-defined change in depth of the annulus (target) appearing in a plane either in front or behind the baseline plane following the cue. Transient disparity changes preceding the cue (distractors) were to be ignored. Stimulus onset asynchrony (SOA) of cue and target was varied (0, 100, 300, or 500 ms). In the control condition, subjects were asked to ignore the fixation colour changes and report the last transient change in depth plane. At 0 ms, SOA subjects were at chance level in detecting a transient change in disparity-defined depth. Performance improved at longer SOAs (> 90% at 500 ms SOA). Subjects' performances were not impaired in the absence of distractors, or in the control condition. Similar to motion detection, a change in disparity-defined depth is also modulated by attentional demands. The 'distractor effect' obtained for both features probably reflects a top-down regulation which parallels recent neurophysiological findings.

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◆ **Flash-induced subjective disappearance of salient visual stimuli**

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Under certain conditions, a salient visual pattern presented at or near the centre of gaze, which would normally be easily seen, can be rendered completely invisible for perception. Combining principles from existing demonstrations of visual suppression, we present here a novel visual stimulus in which the immediate disappearance of highly salient visual patterns can be induced by the presentation of a second, non-overlapping pattern. This effect, which we term generalised flash suppression (GFS), resembles the previously reported binocular-rivalry flash suppression (BRFS) in its dynamic properties, but differs in its spatial requirements. In the main condition, the target is a foveally presented patch or image, shown alone on a black background, and remains continuously visible. After 2000 ms, randomly distributed dots are flashed in the periphery, an event that often causes the immediate perceptual disappearance of the target. While disappearance

is aided by dichoptic presentation, it is neither contingent upon interocular conflict, nor any direct spatial conflict at all. These properties, along with the all-or-none nature of target disappearance, closely resemble the recently described spontaneous target disappearance present in motion-induced blindness (MIB). We characterise several aspects of GFS, exploring its generality, the spatial and temporal requirements for suppression, the role of ocular configuration, and the specificity of adaptation.

[Supported by the Max Planck Society.]

◆ **Further evidence for an inhibitory explanation of transient motion blindness**

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A transient impairment in coherent-motion detection can be induced in normal observers by using a rapid serial visual presentation (RSVP) task. Essential for this effect to occur is the presence of coherent-motion distractors that have to be ignored. We proposed that the resulting motion blindness is caused by a delay in fully releasing inhibition of these distractors. To test this hypothesis, we compared the size of the motion-blindness effect in participants with high and low cognitive inhibition ability. Inhibition ability was inferred from performance on two well-established inhibitory tasks: Stroop interference and negative priming. For the motion task, forty participants viewed two synchronised RSVP streams: a local stream defined by a fixation point changing colour every 100 ms, and a global stream consisting of randomly moving dots. Participants had to detect a red fixation in the local stream (T1), which cued them to attend to the global stream and detect a 100 ms coherent motion episode (T2). In 50% of trials, coherent motion distractors preceded T1, and in 50% T2 was the only coherent motion. Good inhibitors showed significantly more motion blindness than poor inhibitors for motion targets occurring 0 and 100 ms after T1 ($p < 0.01$), but only when T1 was preceded by distractors. This suggests that transient motion blindness is related to the inhibition of distractor motion.

THURSDAY
POSTERS**ATTENTION 2**◆ **How does the brain overcome experimental motion blindness?**

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We investigated the ERP correlates of a transient motion blindness induced in a random-dot kinematogram. Fourteen subjects had to redirect attention from rapid colour changes of a central fixation point to a peripheral coherent motion target with the onset of a predefined colour cue. Motion detection performance was at ceiling level for targets that were presented 400 ms after cue onset. For simultaneous onsets of cue and target, detection performance dropped significantly with increasing numbers of motion distractors—ie 1, 4, or 7 episodes of irrelevant coherent motion presented prior to the colour cue. Event-related brain potentials (ERPs) were recorded to examine the changes in target motion processing brought about by distractor motion. The results indicate that sensory processing, as reflected by posterior N200 amplitude, remained unaffected by increasing numbers of distractors. The N200 was released by a further negative component, peaking over fronto-central electrodes at approximately 250 ms. If only one distractor preceded the target, the negative fronto-central topography collapsed within the next 25 ms. With 4 or 7 distractors preceding the target, however, the described topography persisted for a longer period of time. In conclusion, we propose this ‘frontal negativity’ to be the electrophysiological correlate of a post-perceptual inhibition mechanism that is induced by motion distractors. Release of inhibition, and therefore target detection, appears to be easier when fewer distractors are presented and need to be suppressed.

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◆ **The time course of attentional zoom**

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Notwithstanding the presumption that the notion of an attentional zoom is no more than a useful metaphor, this set of experiments attempts to trace the time course of attentional zooming. The experiments employed an RSVP paradigm where the task was to identify two white target letters (T1, T2 for the first and second targets, respectively) in a stream of black distractor letters. In experiment 1, T1 was a 3 × 3 matrix of identical letters, and T2 a single letter. Assume that the attention lens has to accommodate the whole T1 matrix in order to identify it. Now, when T2 appears as a single letter, there needs to be a change in the spatial extent of attention. The baseline was the case where T1 and T2 were single letters. The results supported this conjecture: performance was poorer when T1 was a matrix, and performance remained poorer up to 600 ms. In subsequent experiments, the shape and size of the configural stimulus (T1) was varied to investigate their effects on the time course of attentional zooming. Beyond 200 ms, the size (radius) of the configuration had little impact, suggesting that the attention changes its spatial extent in a discrete manner. However, when the targets lagged by 200 ms, the size effect was manifest, suggesting that attentional zooming may be characterised as an analogue process.

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◆ **The time course of the attentional blink for objects**

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When attention has to be directed at a first target stimulus (T1), task performance for a second target stimulus (T2) can be worse than in a control condition with the same stimuli but without the need to attend T1. This ‘attentional blink’ (AB) has usually been studied with verbal stimuli (letters and words). We wanted to know whether AB also occurs with figural stimuli (the answer will be “yes”) and whether AB has the same properties (the answer will be “no”). Stimuli were rapid serial visual presentations (RSVP) of target and distractor items (for 100 ms each, with ISI = 0 ms). T1 was a capital letter of the alphabet (A, B, C, ..., Z) which appeared in one of four colours (blue, brown, green, or pink); T2 was a red silhouette derived from a line drawing of an everyday object (1 of 126 silhouettes derived from the Snodgrass and Vanderwart set which were still easy to recognise, as shown by previous research (see Wagemans et al, 1997 *Abstracts of the*

38th Annual Meeting of the Psychonomic Society 2 71, abstract 694); distractors were meaningless silhouettes in blue, brown, green, or pink. T1 was preceded by 9 to 15 distractors; T2 appeared 100, 200, ..., 600 ms after T1 (separated by 1 to 6 distractors); after 1 to 3 additional distractors, the response screen appeared. In the experimental condition, subjects had to report the identity and colour of T1 as well as the identity of T2. In the control condition, subjects received the same RSVP streams but had to report only the identity of T2. Identification of T2 was significantly more difficult in the experimental condition when T2 appeared 100, 200, and 300 ms after T1 (not for longer intervals). This time course differs from the AB for letters where it follows a more U-shaped function.

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◆ **The effect of attention on the speed of information processing**

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Covert spatial attention has been shown to improve performance on several perceptual tasks. Recent work (McElree and Carrasco, 1999 *Journal of Experimental Psychology: Human Perception and Performance* 25 1517–1539; Carrasco and McElree, 2001 *Proceedings of the National Academy of Sciences of the USA* 98 5363–5367) has demonstrated that, in addition to enhancing the signal, covert attention also speeds up the rate at which visual information is actually accrued. Using the response-signal speed–accuracy trade-off (SAT) procedure, we conducted two experiments to assess the effect of attention on the speed of information processing in an orientation-discrimination task. In addition to measuring accuracy and response time, we also simultaneously recorded event-related brain potentials (ERPs) to determine the locus of any attentional effect within the information-processing stream. For both experiments, accuracy of the orientation decision was higher for cued than uncued spatial locations. However, there were no significant differences between the cued and uncued conditions in the rate and intercept parameters of the SAT function. Also, a latency analysis of the lateralised readiness potential and of sensory ERPs revealed no cueing effects in premotoric and motoric processing times. Consistent with previous research, however, early ERP components were enlarged in amplitude at cued as compared to uncued locations. Altogether, whereas these latter ERP results indicate an effect of spatial attention on perceptual processing, we found no evidence for an acceleration of visual information processing with attention. It is conceivable, though, that covert attention speeds up the rate of visual information accrual in attentionally more demanding tasks.

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◆ **Change blindness effects in virtual starfields**

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In contrast to the subjective impression of a richly detailed representation of our visual environment, several studies have revealed difficulties in detecting changes introduced on the background of global interruptions of scene perception. Our previous work on this change blindness phenomenon [Dornhoefer et al, 2002, in *The Brain's Eyes* Eds J Hyönä, D Munoz, W Heide, R Radach (Oxford: Elsevier) pp 119–131; Velichkovsky et al, 2002 *Transportation Research, Part F* 5 99–109] showed differences with respect to overall static and dynamic conditions of presentation as well as occlusion modes. To further investigate these differences, we developed a new method based on computer-generation of three-dimensional starfields. Simulated self-motion flights served as the dynamic condition, whereas the static scenario consisted of corresponding screenshots. Subjects were instructed to respond to a single appearing or disappearing object by pressing a mouse button. Online analysis of their eye movements allowed gaze-contingent changes during saccades and during blanks produced within fixations. In half of the blank trials, no changes were made to avoid guessing. Additionally, changes could occur during fixations without blanks as control condition. A pronounced change blindness effect was found for both occlusion modes. Furthermore, detection rate and reaction time differences were again discovered for the static and dynamic conditions.

◆ **The suboptimality of attentional weighting across precue validities**

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In a simple standard cueing task (Posner, 1980 *Quarterly Journal of Experimental Psychology* 32 3–25) an observer detects a signal at one of two locations while a precue indicates the probable signal location. A cueing effect (valid > invalid) is typically found, and is often attributed to a limited-capacity attentional mechanism. This attribution is challenged by an optimal (Bayesian)

observer with unlimited capacity, as it predicts cueing effects, and also describes human performance in some cueing tasks (Eckstein et al, 2002 *Journal of Vision* 2 25–45; Shimozaki et al, 2003 *Journal of Vision* 3 209–229). A Bayesian observer, in using all prior information, differentially weights information at the two locations by precue validity; thus, this predicts increasing cueing effects with increasing validity. To test validity effects, observers performed a YES/NO contrast discrimination of a 50 ms Gaussian signal (contrast = 6.3%, pedestal contrast = 6.3%, SD = 12.4 min of arc) presented in white noise (mean = 25.0 cd m⁻², SD = 2.93 cd m⁻²) and appearing at one of two locations (eccentricity = 2.5°). The validity of a 150 ms precue at one location was varied from 50% to 90%. Precues were presented either centrally or peripherally, and feedback indicated either signal location or correctness. There were three main results: (1) Cueing effects did not change with validity, contrary to Bayesian observer predictions. (With signal location feedback, cueing effects increased somewhat with validity, apparently due to increased trial-to-trial knowledge of precue validity.) (2) Observers varied greatly in their cueing effects. (3) Cueing effects were much larger for the peripheral cues, compared to central cues. Thus, observers appeared to select attentional strategies automatically, based only on cue type and the specific observer, and disregarding the optimal weighting of information by validity. [Supported by NIH 53455, NASA NAG-1197, NSF-0135118.]

◆ **Psychophysics of search for multiple targets**

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Human performance in visual search for a single target object can be well accounted for by models based on signal detection theory (SDT; eg Palmer et al, 2000 *Vision Research* 40 1227–1268). Is it possible to generalise the same ideas to subitising task when observer has to detect multiple identical targets simultaneously? Two experiments are reported where observers had to discriminate between displays with n and $n - 1$ targets (bright dots) among a larger number of distractors (dim dots). Luminance difference thresholds for 75% correct were measured for different numbers of targets and distractors. The thresholds for multiple targets ($n = 2$ to 4) were 1.2 to 1.5 times higher than for a single target (usual visual-search task). Straightforward extension of SDT-based model would predict threshold for 1-target versus 2-targets task about 1.1 times higher as compared with search for a single target. The effect of the number of distractors was found to be almost independent of the number of targets, and consistent with SDT models. The results can be explained by a second stage of processing that is unable to use all information present at the first stage.

◆ **Temporal dynamics of perceptual decision**

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To fully characterise the temporal dynamics of perceptual decision, we combined the external noise method with the cue-to-respond speed–accuracy trade-off (SAT; Doshier, 1976 *Cognitive Psychology* 8 291–310) paradigm, and elaborated the perceptual template model (Lu and Doshier, 1999 *Journal of the Optical Society of America* 16 764–778) with a dynamic decision process. We manipulated the amount of external noise added to the signal stimulus, the contrast of the signal stimulus, and the report cue delay. Specifically, observers identified the orientation of one of eight briefly presented peripheral Gabor targets (± 12 deg). The target location was cued 234 ms before its onset; an auditory beep cued the observers to respond as quickly as possible. Eight cue delays and five Gabor contrasts were tested in two external noise conditions. In all external noise and signal contrast conditions, d' increased as a function of processing time (PT). Moreover, all the d' versus PT (SAT) functions were well fit by exponential functions with identical time constant and intercept but different asymptotic levels. The result suggests that, despite enormous range of external noise and signal contrast, and in the ultimate accuracy of performance, information accumulated with the same rate and starting time across all the external noise and contrast conditions. Data from the standard-response-time version of the experiment conducted before, halfway, and after the SAT procedure were consistent with the speed–accuracy trade-off data. A simple elaboration of the perceptual template model with a dynamic decision process in which information accumulates with the same rate but with step sizes proportional to the signal-to-noise ratio in the perceptual representation of the visual input fully accounts for the results.

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MOTION—HIGH LEVEL

◆ Chromatic mechanisms for the perception of global and biological motion

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We investigated the contributions of colour to the perception of globally moving random-dot kinematograms and of biological motion. In both experiments, the stimulus consisted of signal dots and noise dots. In the global-motion task, the signal dots were defined by a uniform global motion in one of four possible directions. The noise dots were moving incoherently in a random direction. In the biological-motion task, the signal was defined by 104 points from the surface of a walking person. The noise dots were chosen randomly from a set of walkers moving in a variety of different directions. In both tasks, the colour of signal and noise dots were independently varied in the isoluminant plane of DKL colour space. For each colour combination, the signal-to-noise ratio was determined by an adaptive staircase procedure where the subjects could reliably identify the direction of motion of the signal dots. In both tasks, there was a significant contribution of colour to the identification of the direction of motion. The contribution increased with the chromatic difference between signals and noise dots. The resulting tuning function for biological motion was narrower than the one observed for global motion. We conclude that colour can play an important role in motion perception, and even more so in perceiving shape from motion.

◆ 3-D perception of biological motion in different orientations from a flat display

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A moving human or other animal projected onto a flat image plane and represented only by a few points evokes a vivid percept of a three-dimensional (3-D) moving body. This percept of biological motion arises rapidly and automatically. People not only readily recognise such moving dot patterns from the side, but also in any other orientation in depth. It is believed that specialised brain areas are responsible for the percept in different orientations. If this is true, people should be able to accurately judge the 3-D orientation in depth of a flat biological-motion stimulus. We describe several experiments on the robustness of heading judgments with respect to parameters such as shown body parts, distortions of the body, and the availability of local motion information. We manipulated the amount of motion and path information of points on the body by relocating them after a short interval. Such a manipulation distorts dynamic depth perception, as we showed for stimuli in which a distorted (scrambled) walker was presented. We compared the results for judgments of walking persons and for scrambled versions of the same stimuli. The judgment of heading turned out to be remarkably robust and accurate in all conditions.

◆ Category effects and orientation specificity in inverted and upright displays of biological motion

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The visual recognition of human actions in biological-motion displays has been shown to be orientation-specific. Using short-term priming, Verfaillie (2000 *Brain and Cognition* **44** 192–213) found significantly more priming for congruent in-depth displays than for displays that differed in their in-depth orientation. Pavlova and Sokolov (2000 *Perception & Psychophysics* **62** 889–899) used a long-term priming paradigm and found similar effects when displays were rotated in the frontoparallel plane. The priming effect, however, was limited to congruent upright displays. Pavlova and Sokolov failed to find a pronounced priming effect for congruent inverted displays. While the congruency effect for in-depth displays appears to hold for right-facing and left-facing point-light walkers, it appears to hold only for upright-oriented congruent displays. We addressed this issue of orientation specificity for inverted displays using a short-term priming paradigm similar to that of Verfaillie (2000). In addition to a point-light walker, we also used two other actions in order to find whether priming would vary as a function of orientation, congruence, and type of action. Subjects were presented with either upright, inverted, or 'neutral' displays and then responded by indicating whether they thought the display was presented upright or inverted; there was no feedback. An analysis of the reaction times revealed significantly greater priming for congruent displays than for incongruent displays. Similar levels of significant priming were found for both upright and inverted congruent displays. A significant 3-way interaction also suggests that the different actions tend to prime themselves and other actions differently in the context of orientation and congruence.

◆ **Biological movements and the perceptual binding problem**

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The modular doctrine of vision (Zeki and Bartels, 1998 *Philosophical Transactions of the Royal Society of London, Series B* **353** 1911–1914; Zeki and Bartels, 1998 *Proceedings of the Royal Society of London, Series B* **265** 1583–1585; Aleksander and Dunmall, 2000 *Proceedings of the Royal Society of London, Series B* **267** 197–200) holds that different attributes of the visual scene are processed by dedicated functional modules. Previous studies provided evidence of such a specialisation by showing that the visual attributes of simple stimuli—such as colour, form, and movement—are not detected synchronously. In particular, Viviani and Aymoz (2001 *Vision Research* **41** 2909–2918) used simple geometrical stimuli to show that movement onset is perceived 70 ms after a change in colour or shape. This asynchrony raises the problem of how the perceptual components of the image are made to coalesce into a unitary conscious experience. In this study, we explored the possibility that, at least in the case of movement and colour, one binding factor is the biological nature of the movement. Rather than computer-generated stimuli, we presented a video clip of a real hand picking up a billiard ball with a natural grip. We modified the original clip so that the colour of the ball switched from green to red or vice-versa at various intervals, either before or after the ball started moving. Participants had to indicate whether the change in colour had occurred before or after movement onset. With the help of a psychophysical model, response probabilities were translated into an estimate of the delay with which colour and cinematic changes reached consciousness. Unlike for the artificial stimuli used previously, there was no asynchrony between the perceived changes in colour and kinematics. The fact that movement is ostensibly caused by a natural biological action is sufficient to set into register the outputs of the modules that process colour and movement information. The finding is discussed within the framework of the theory of event coding (Hommel et al, 2001 *Behavioral and Brain Sciences* **24** 849–937).

◆ **Perceiving emotion from point-light displays of interpersonal communication behaviours**

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Point-light displays of the human form provide sufficient information to recognise useful properties of the actor and actions being represented. Although it is now well established that observers can identify properties such as gender and affect from a single actor (eg Dittrich et al, 1996 *Perception* **25** 727–738), it remains to be established how interpersonal interactions are interpreted. A database of point-light displays was collected from pairs of female and male actors who together performed short vignettes expressing different emotional states (anger, joy, sadness, romantic love, and fear). Presentations of these displays in their natural dyadic form, along with presentations where one of the actors was occluded (monads) and presentations where the image of this single point-light actor was reflected to create a mirror image of the actor (reflected dyads), were shown to participants who were asked to judge the emotional content. Results for recognition of different emotions varied depending on the type of presentation viewed. It was found that for joy, viewing the natural dyads improved recognition over the monads, whereas for sadness the opposite was true. Anger and fear recognition were unaffected by display condition. Performance for the reflected presentations of love was good and was similar to that of the natural dyads acting this emotion. However, monad ratings for this emotion were at chance levels. These results suggest that the efficiency of emotion recognition in dyads compared to monads is strongly dependent upon the type of emotion portrayed. Furthermore, the interpersonal context in which point-light displays of human movement are presented affects fundamentally the attribution of emotion to the actions portrayed.

◆ **Is form information necessary for the recognition of point-light walkers?**

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Many classical studies rely on the assumption that the perception of point-light stimuli is based on the analysis of motion information. A recent experiment by Beintema and Lappe (2002 *Proceedings of the National Academy of Sciences of the USA* **99** 5661–5663) seems to challenge this classical view. Subjects can perceive reliably the direction of walking from a new type of

point-light stimulus (sequential position stimulus, SPS) with strongly impoverished local-motion information. This stimulus was generated by randomising the dot positions on the skeleton of the walker. This suggests that form, rather than local motion information, is critical for the perception of point-light stimuli. We present experimental and computational evidence that suggests a different interpretation of this experiment: (i) We show that there is substantial residual motion information in the SPS, which is sufficient for a reliable detection of walking direction. We also show that a recognition performance close to psychophysical results can be achieved by extracting this information with simple physiologically plausible neural detectors. (ii) We present a new type of point-light stimulus (critical feature stimulus, CFS) that matches closely the low-level properties of the SPS, but which is incompatible with the kinematics of a human body. In spite of this fact, recognition performance is comparable to the SPS. This result seems to contradict recognition of point-light walkers by reconstruction of body shape from the dot positions. A physiologically plausible account for both experimental results is provided by the hypothesis that point-light stimuli are recognised by detection of specific spatial arrangements of opponent-motion features.

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◆ **The perception of contours, real or subjective, enhances velocity discrimination**

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We studied the performance of human subjects for angular velocity discrimination in five varieties of motion stimuli. Motion is defined by real luminance edges in the first variety and by subjective colour spreading in the second variety. Keeping average luminance constant for the rest of the stimuli, motion is defined by contrast modulation to a static field of random dots in the third variety, by contrast modulation of a field of dynamic random dots in the fourth variety, and by isoluminant colour changes in the last variety. Two classes of velocity discrimination thresholds were found. The higher threshold is approximately ten times that of the lower one. Interestingly, the higher threshold is consistently associated with the absence of the perception of well-defined contours in the motion stimuli. Moreover, keeping the average luminance constant throughout the stimuli does not always produce high discrimination thresholds. Contours, real or subjective, appear to be fundamental for the estimate of motion parameters such as velocity.

◆ **The bias in acceleration perception for simulated motion in depth**

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For motion in the frontal plane, acceleration is perceived with bias, i.e. motion having constant velocity is perceived as decelerated (Runeson, 1974 *Psychological Research* 37 3–23). We examined whether such a bias can also be observed with motion in depth. In the first experiment, different accelerations of target approaching and receding were simulated on a CRT screen by optical expansion or contraction of a 2-D grey square on a black background. Only monocular information was accessible to observers for assessing whether motion had negative, zero, or positive acceleration. For expansion to be recognised as a constant-velocity approach, target had to decelerate, and for contraction to be recognised as a linear recede, target had to accelerate. In the second experiment, we examined how object texture, ground texture, and height in visual field affect the bias in acceleration perception for the approaching target. All the factors exhibited significant effects: the first two reduced the bias, and the last one even changed the sign of the bias, making it similar to the one observed in the frontal-plane motion. The results are discussed in terms of information-integration theories and the relation between 2-D and 3-D motion perception.

◆ **The effect of spatial limitations on speed discrimination in global motion**

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Research with global dot motion (GDM) stimuli has shown that coherence of global motion can be detected when signal dots comprise as few as 5%–10% of the total dot number. We investigated how global-motion coherence thresholds are affected by the dot speed. The stimuli were circular (radius: 6 deg) consisting of 100 dots with signal dots moving to simulate radial motion across the eight, 50 ms, frame sequence. A two-interval forced-choice procedure was used in conjunction with a staircase to determine coherence thresholds for radial motion with speeds from 1.2 to 24 deg s⁻¹. The motion detection threshold remained constant at approximately

10 dots for speeds less than 9.6 deg s^{-1} . For greater speeds, thresholds increased so that by a dot speed of 24 deg s^{-1} the threshold had doubled. However, in order to produce a range of speeds, the magnitude of the dot jump on each frame was changed ($0.06\text{--}1.2 \text{ deg frame}^{-1}$). The dot jump-size may account for the results, since the receptive field size of local motion detectors is small and thus unable to extract large dot jumps. Thresholds may increase in order to offset the probability that some intended dot movements are not adequately extracted. The experiment was repeated so that the same range of dot speeds was produced with a range of small dot jumps ($0.17\text{--}0.67 \text{ deg frame}^{-1}$); global-motion sensitivity then remained unchanged. A procedure which extracts local motion signals as nearest-neighbour pairs is effective in accounting for the change in motion sensitivity as a function of the dot jump-size.

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◆ **Depth stratification induced by illusory surfaces interferes with motion integration**

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We have studied the effects of global context on motion integration. We used two Gabor patches, and in the experimental condition one of them was surrounded by inducers that created an illusory surface. We used a 2IFC paradigm, and in the standard interval the gratings translates at a constant speed of 3.6 deg s^{-1} . We reported earlier that speed discrimination thresholds increase when one of the motion signals is perceived on top of an illusory surface (compared to a control configuration), and we concluded that the presence of an illusory figure interferes with the integration process (Mosca et al 2002 *Perception* 31 Supplement, 85; Vergheze and Stone, 1995 *Vision Research* 35 2811–2823). There are two aspects of illusory surfaces: the formation of a surface and the depth stratification that brings the surface nearer than the inducers. To test which is the critical factor for motion integration, we ran a new series of experiments. When the inducers have binocular disparity information, which places them either in front or behind the Gabor, the patch is not perceived as connected to the surface and no change in threshold is found. Even more critically, when both motion signals are perceived as belonging to two distinct illusory surfaces, thresholds are not different from the control condition. Therefore, surface formation is not the critical factor, but rather it is the location of the motion signals on different depth planes that interferes with motion integration.

◆ **The force of appearance: Gamma movement, impetus, and representational momentum**

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In the launching effect [Michotte, 1963 *The Perception of Causality* (New York: Basic Books)], a moving launcher contacts a stationary target, the launcher becomes stationary, and the target begins to move. In naïve impetus theory, setting an object in motion imparts impetus that maintains motion until the impetus has dissipated [McCloskey, 1983, in *Mental Models* Eds D Gentner, A L Stevens (Hillsdale, NJ: Lawrence Erlbaum Associates)]. In representational momentum, memory for target position is displaced in the direction of target motion (Hubbard, 1995 *Psychonomic Bulletin & Review* 2 322–338). Hubbard and Ruppel (2002 *Visual Cognition* 9 153–176) reported representational momentum of targets in launching-effect displays is less than representational momentum of nonlaunched control targets, and they suggested this reflects expectations a launched target would become stationary after impetus imparted from the launcher dissipated. Such an account suggests that attribution of impetus (rather than launcher motion) produces the launching effect. Illusory gamma movement may produce attribution of impetus in the absence of launcher motion if a stationary launcher appears adjacent to a target that immediately begins to move. In experiment 1, a stationary launcher appeared adjacent to a target, and target displacement decreased if the launcher appeared when target motion began or if target motion was in the direction of impetus. In experiment 2, the target remained stationary, and target displacement was not influenced by the launcher. Results suggest the launching effect results from (a) attribution of impetus imparted from the launcher rather than from launcher motion (see also Hubbard and Favretto, 2003 *Psychological Research/Psychologische Forschung* 67 134–152), and (b) cognitive influences rather than direct perception.

◆ **Adaptation to high-level motion without awareness**

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When a single moving stimulus is presented in the peripheral visual field, its direction of motion can be easily distinguished, but when the same stimulus is flanked by other similar moving stimuli, observers are unable to report its direction of motion. In this condition, known as 'crowding', specific features of visual stimuli will not access conscious perception. The aim of this study was to investigate whether adaptation of high-level motion-processing areas is preserved in crowding conditions. Logarithmic spirals, similar to those used by Cavanagh and Favreau (1980 *Perception* 9 175–182) were used as adapting stimuli. A rotating spiral stimulus (target spiral) was presented, flanked by spirals of the same type, and observers were adapted to its motion. The observers' task was to report the rotational direction of directionally ambiguous motion (test stimulus) presented afterwards. The directionally ambiguous motion consisted of a pair of spirals flickering in counterphase, which were mirror images of the target spiral. Although observers were not aware of the rotational direction of the target and identified it at chance levels, the direction of rotation reported by the observers (motion aftereffect) was contra-rotational to the direction of the adapting spiral. Since all contours of the adapting and test stimuli were 90° apart, local motion detectors tuned to the direction of the mirror-image spiral should fail to respond, and therefore not adapt to the adapting spiral. Thus any motion aftereffect observed should be attributed to adaptation of high-level motion-processing areas responding to complex configurations of moving stimuli. Since rotation-selective cells are located in area V5a/MST, it is concluded that activation of this area is insufficient for conscious perception.

LOW-LEVEL PROCESSES—COLOUR

◆ **A novel approach for luminance and opponent chromatic coding**

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There are many information-theory studies justifying the coding of L, M, and S signals coming from cones into luminance and opponent chromatic signals. Buchsbaum et al (1983 *Proceedings of the Royal Society of London, Series B* 220 89–113) show that this coding offers an optimal representation of light because it corresponds to a decorrelation of L, M, and S signals. Actually this coding exploits the spatial and chromatic redundancy of natural images as measured by cones and guarantees a reduction of the information carried by the optic nerve (Lee et al, 2002 *Vision Research* 42 2095–2103). But these studies do not take into account that there is only one cone type at each spatial position in the retina. We show that sampling one colour sensitivity per spatial location can be written as the sum of a luminance signal and a sub-sampled opponent chromatic signal, independently of the arrangement of the different cone types (random or regular). Luminance is not subject to sub-sampling (it is defined with maximum acuity), whereas opponent chromatic signals are sub-sampled accordingly to the arrangement of cones. In random arrangement, the composition of the luminance signal (ie the proportion of L, M, and S) for optimising spatial resolution depends on the local arrangement of cones, which determines also the amount of L, M, and S in chromatic opponent signals. Therefore, considering the global cone signal, we show that luminance and opponent chromatic signals resemble luminance and opponent colours as predicted by psychophysics. This confirms that the chromatic oppositions are initiated in the retina level by the cone sampling process, which makes explicit the relation between the response of retinal neurons and the opponent colours observed in psychophysics.

◆ **Spectral bandwidths for the detection of colour within random colour textures**

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We investigated the spectral properties of colour detection mechanisms via a noise masking paradigm. Contrast detection thresholds were measured for equiluminant chromatic modulations in the [L-M,S-(L+M)]-plane within a random texture. Each texture image was the spatial juxtaposition of colour samples drawn from a bidimensional probability density function whose support was a sector in the equiluminant plane. The task consisted in the detection of an

equiluminant signal of Gaussian shape ($\sigma = 1.25$ deg) whose amplitude was the chromatic signal and whose pixel-wise chromaticity was spatially modulated by the noise. Each stimulus consisted of two textures ($5 \text{ deg} \times 5 \text{ deg}$) arranged side-by-side and separated by a gap (width = 0.5 deg) with the same chromaticity as the uniform background. Subjects were asked to judge, via a 2AFC paradigm, on which side of the central fixation point the signal was displayed. Contrast thresholds were measured for four colour directions and three sector widths at increasing levels of the average energy of the axial component of the noise. Results show that contrast thresholds are unaffected by the width of the noise sector, as previously found for temporally modulated stimuli (D'Zmura and Knoblauch, 1998 *Vision Research* **38** 3117–3128). The results are consistent with the existence of spectrally broadband linear detection mechanisms tuned to the signal colour direction and support the hypothesis of the existence of higher-order colour mechanisms with sensitivities tuned to intermediate directions in the colour space.

◆ **The effect of spatial frequency on colour appearance: Colour contrast versus high-spatial-frequency tritanopia**

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Neutral strips against a coloured background may change their appearance. It is believed that they exhibit chromatic contrast for low spatial frequencies, and assimilation for high spatial frequencies. While having corroborated chromatic contrast for a low frequency, we found high-spatial-frequency tritanopia rather than assimilation for a high frequency. The colour monitor screen was divided into two regions. In the upper region, neutral, horizontal, equally spaced (distance between strips was 0.13, 0.25, 0.40, and 2.00 deg to give spatial frequencies of 8, 4, 2.5, and $0.5 \text{ cycle deg}^{-1}$) test strips were presented on coloured backgrounds ($3.2 \text{ deg} \times 5.2 \text{ deg}$). The width of the strips was a quarter of the distance between them. Observers adjusted the colour of the matching bar presented on the neutral background below, to that of the colour of the strips. Twenty-four chromaticities (evenly distributed across the colour gamut triangle) of the backgrounds in the ML plane and thirty in the equiluminant plane, were tested. Five matches were made for each frequency and each background chromaticity. Viewing was binocular. In accord with the previous results, for the low-frequency ($0.5 \text{ cycle deg}^{-1}$) strips, the backgrounds were found to induce the colour complimentary to that of the background. For the high-frequency ($8 \text{ cycles deg}^{-1}$) strips, most backgrounds induced only unique hues (yellow, blue, and green), with a few backgrounds inducing a mixture of green with either yellow or blue. Neither colour contrast, nor assimilation was observed for the strips of $8 \text{ cycles deg}^{-1}$. These results are in line with an account of high-spatial-frequency tritanopia (Logvinenko, 2001 *Perception* **30** 223–232) that argues this colour illusion is a result of poorer spatial resolution of the post-receptor channels that are driven by the S-cones.

◆ **How many spectral basis functions do red – green dichromats need to discriminate surface colours under different lights?**

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For observers with normal colour vision, reflectance spectra can be adequately represented by linear models with at least five basis functions in tasks requiring the discrimination of Mondrian-like coloured patterns of Munsell papers. This number of basis functions is needed whether the patterns are presented under the same or different illuminants (Oxtoby et al, 2002 *Perception* **31** Supplement, 66), which may be important in understanding surface-colour perception. Fewer basis functions should be needed, however, for dichromats, who have just two distinct cone classes, but it is unclear whether the number of basis functions would be reduced still further across an illuminant change. Accordingly, red – green dichromatic observers were presented with computer simulations of pairs of Mondrian-like coloured patterns comprising 49 (7×7) abutting 1-deg square Munsell papers in which in half of the trials the spectral reflectances of the surfaces were replaced by an approximation with a variable number of basis functions. Observers had to report whether the two patterns consisted of identical papers. In different blocks of trials, the two patterns were illuminated by the same or different daylight with correlated colour temperatures of either 6700 K or 25000 K. It was found that for both protanopes and deuteranopes, three basis functions were needed whether the illuminant was the same or different across the patterns. This reduction seems to be a consequence of the poorer colour-discrimination ability of these observers, rather than impairment in surface-colour perception.

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◆ **Illusory Brewster's colours and resolution in the red – green opponent channel**

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A midget ganglion cell in the primate retina is a unit of fine spatial vision as well as the main element of the red–green opponent channel. Such 'double duties' cause confounding the colour and spatial information. In particular, they result in the appearance of illusory Brewster's colours while viewing an achromatic grating of high spatial frequency and high contrast. D R Williams, D H Brainard, and their colleagues [Williams et al, 1993, in *From Pigment to Perception* Eds A Varlberg, B Lee (New York: Plenum Press)] showed that the Brewster's colours phenomenon originates in the irregular arrangement of cones in the retina mosaic. However, the possibilities of reducing the illusory colours by subsequent processing in any post-retinal structures remain unclear. For quantitative investigations of such processing, a computational static linear model of the midget pathways in the central primate retina was constructed. The model comprises about 3300 neurons: cones of L- and M-type with coordinates, taken from the description of a segment of the real macaque retina; midget bipolar and ganglion cells; horizontal cells of H1-type and narrow-field amacrine cells. It was found that a simple post-retinal filter of low spatial frequencies, having characteristics that conform to visual resolution in the red–green channel, provides considerable reduction of parasitic red–green opponent signals and, in particular, weakening of the Brewster's colours. [Supported by the Russian Foundation of Basic Research Grant 01-04-48632.]

◆ **Colour assimilation in Munker – White patterns: Asymmetric shifts in hue and saturation for blue and yellow flanking conditions**

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When short coloured target bars are placed within more extended differently coloured flanking bars, the perceived colour of the target bars shifts dramatically towards the colour of the flanking bars (Munker–White effect). We measured this effect comparatively for blue and yellow flanking conditions. A calibrated colour CRT display (Eizo monitor with standard RGB) served for computer-assisted stimulus presentation and adjustment. Stimuli were 36 thin (11.2 min) horizontal bars (8.2 deg) alternating in colour (blue/yellow); part (2.15 deg) of the yellow or blue bars was replaced by eight red bars so that two rectangular areas were formed, to the left and right, separated by 1.8 deg. Six emmetropic, colour-normal observers adjusted the colour of the target in one rectangle to match it with that in the other. Settings (RGB data) were transformed into CIE Lab (uniform colour space) values. The results indicate symmetric shifts in brightness (reduction by blue, enhancement by yellow flankers), but asymmetric shifts in hue and saturation. Saturation was enhanced in both conditions, but approximately twice as much with yellow as with blue flankers. Hue shifts were more pronounced (by a factor of 1.4) for blue flankers (towards purple) than for yellow flankers (towards orange). These asymmetries are consistent with the notion that the yellow–blue colour opponent mechanism is split into two subsystems (eg Sankeralli and Mullen, 2001 *Visual Neuroscience* **18** 127–135) with different spatial-frequency characteristics (Hutchinson and Logvinenko, 2002 *Perception* **31** Supplement, 66).

◆ **Chromatic adaptation across depth planes**

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Mid-spectral adaptation is tuned to geometrical features of a scene, such as spatial frequency and orientation (Werner, 2003 *Vision Research* **43** 1611–1623). The purpose of the present study was to investigate whether the spatial structure of the background exerts an influence on chromatic adaptation across depth planes. The stimuli were produced on a calibrated colour monitor. They were in standard condition (D65) achromatic ($u' = 0.197$, $v' = 0.468$; luminance mean = 19.3 cd m^{-2}) and consisted of two identical, segmented background patterns ($10.6 \text{ deg} \times 11 \text{ deg}$). The patterns were binocularly fused and the perceived depth relation between the central test field and the background was produced by introducing retinal disparity. Chromatic adaptation was measured for the transition from D65 adaptation to green adaptation (equiluminant chromaticity shift along the L/M axis, $\Delta E_{uv} = 21.2$). The effect of adaptation ($t = 5 \text{ s}$) was measured by a hue cancellation technique for the achromatic appearance of the central test field, whereby test field and background were perceived in one of six different depth planes (zero disparity or crossed disparity 1.9–28.5 min of arc). It was found that the influence

of the background on adaptation of the test field decreased with increasing disparity. It is proposed that this mechanism supports the perceptual organisation and colour constancy in 3-D scenes. [Supported by University of Tübingen Fortune programme (#1059-0-0) and DFG (WE1710/1-1).]

◆ **Is glare spectrally selective?**

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Glare depends on intensity, space, and time (Vos, 1999 *CIE 24th session, CIE Publ.* **133** 38–42). Disability glare is explained as a veil that reduces retinal contrast (IJspeert et al, 1990 *Vision Research* **30** 699–707). Discomfort glare causes discomfort without impairing vision. Because subjects often report to prefer chromatic illumination, we address the question of a possible spectral effect of glare caused by peripheral and steady illumination. Observers were screened for contrast sensitivity function (achromatic CSF, eight spatial frequencies, 6 deg Gabor target) to assess disability glare and for subjective comfort scaling (5-point rating system) to assess discomfort glare. A large glaring colour field (50 deg × 42 deg, > 200 cd m⁻²) was surrounding the test field (14 deg × 10.5 deg, 30 cd m⁻²). A blue/yellow/orange comparison and a red/green/reference (achromatic grey control surround, 30 cd m⁻²) comparison were performed during independent long 20 min sessions, and a red/green comparison during interlaced short 10 min sessions. With long adaptation periods, various colour glaring fields have significantly different effects on contrast sensitivity at low and at high spatial frequency. The blue and green glaring fields impair the CSF at low spatial frequency, but slightly improve it at high spatial frequency. Comfort evaluation yields lower rating for red and orange adaptation. No significant spectral effect was found with the rapid screening procedure. The opposite variation of contrast sensitivity at low and at high spatial frequency suggests that the origin of discomfort cannot originate from a veiling glare. The parallel decline of CSF at long wavelength and impairment of comfort suggest the addition of spectral content as a fourth dimension to glare which might interact with the spatial dimension.

◆ **Experience-dependent development and plasticity of colour constancy in guppies (*Poecilia reticulata*)**

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Without functioning of the mechanisms of colour constancy, colour vision loses its biological essence. In our experiments, the postnatal development of the mechanisms of colour constancy has been investigated with consideration of individual visual experience. Experiments were carried out on the fish (*Poecilia reticulata*), which were born and raised in the following different visual environments: (1) Regular colour environment, in conditions of unaltered spectrum of illumination—the aquarium, in the daytime, was illuminated for 14 h with a 100 W incandescent lamp; 10 h comprised 'night'. (2) Anomalous colour environment: (a) in aquarium with opaque white walls; (b) in aquarium with black walls; (c) in aquarium with red walls. The illumination was with a 100 W incandescent lamp for a 14 h 'day', with a 10 h 'night'. (3) The control animals were born and raised in natural conditions. All three groups of the fish were trained to discriminate the colours in conditions of changing spectral content of illumination. Experiments have shown that in all experimental groups of the animals, there were significant alterations in the colour constancy function, as compared to the control group animals. Further transfer of the animals into the conditions with natural illumination, for 1 month, restored the altered function. The only difference was found in the 2c group animals that were raised in conditions of predominant loading of the red receivers. In this group the function did not recover to the full extent. It is suggested that functions of colour constancy belong to those functions the full development of which requires accumulation of individual visual experience.

◆ **Effects of luminance and colour contrast on visual search and reading**

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We investigated the effect of luminance contrast on the speed of visual search and reading when characters and background differed with respect to colour. Subjects were required to search for target letters in 7 × 7 arrays of green characters on a grey background. In an additional experiment, subjects were required to read texts aloud and their reading rate (words per minute) was

measured. In both experiments, the luminance of the grey background was held constant (22 cd m^{-2}), while the luminance of the green characters was varied from dark to bright-green (about $2-55 \text{ cd m}^{-2}$). The colour contrast between grey background and green characters was nearly constant in all conditions. During visual search, eye movements were recorded by means of a video eye tracker with a sampling rate of 250 Hz. With increasing character luminance, search times, number of fixations, and mean fixation duration first increased and then decreased. The maximum occurred when characters and background were approximately equiluminant. Saccade amplitude was not affected. The effects were largest for small characters (0.17 deg), but occurred also for medium (0.37 deg) and large (1.26 deg) characters. Reading rate decreased strongly when characters and background approached equiluminance. Thus, moderate colour contrast is not sufficient for effective visual search or reading, if simultaneously the luminance contrast between characters and background is small. The finding may be due to the fact that at high spatial frequencies contrast sensitivity for pure colour information is considerably lower than for luminance information.

LIGHTNESS, BRIGHTNESS, SHADING, TRANSPARENCY

◆ **Spotlight size determines lightness**

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Previous research (Zdravković and Gilchrist, 2001 *Perception* 30 Supplement, 18) showed that for objects covered with two illumination levels, lightness is computed on the basis of (i) the assigned sign of the illumination (ie spotlight versus shadow) and (ii) the area that each illumination covers. A series of five experiments that specify the relationship between the area size covered with spotlight and the lightness judgment is reported. A display made of five adjacent rectangles ($11 \text{ cm} \times 22 \text{ cm}$), spanning in range from black to white, was suspended in mid-air. The upper part of the display was covered with spotlight, leaving the lower part of the display in the room illumination. The area covered with the spotlight was varied (3 cm to 14 cm). The edge between the two illumination levels was sharp. Subjects estimated lightness of the whole rectangles and of the parts in the different illumination levels. As in previous research, the new data show that lightness judgment depends on the size of the spotlight region. The new experiments show that if the spotlight covers two-thirds or more of the object, its lightness is computed on the basis of the part in the spotlight; when the spotlight covers half of the object, its lightness is a compromise between the two regions in different illumination; finally when the spotlight covers a quarter or less of the object, its lightness is completely based on the part in the room illumination. A linear function fits the obtained data.

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◆ **Effects of articulation on lightness depend on the spatial arrangement of the surround**

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It has been claimed that increasing the articulation (ie the number of surfaces) in a visual scene leads to a more accurate perception of the true reflectance scale. On an LCD monitor, we manipulated articulation in a display that consisted of two 5 deg disk-and-ring patterns by varying the number of rings surrounding the target disk, while keeping the surround size constant. Three observers adjusted the luminance of the matching disk to achieve a lightness match to the target. Four experiments were performed in which the target was either lighter or darker than its immediately surrounding ring and the surround rings were ordered either in a 'wedding cake' arrangement, in which the ring luminances increased in a stepwise fashion from the outside to the inside of the surround, or in an 'amphitheatre' arrangement, in which the ring luminances decreased from the outside to the inside. Each experiment included a low-articulation condition and a high-articulation condition. The luminance range within the surround was held constant across all conditions. We found an effect of articulation on the target lightness. The direction of the effect depended on the arrangement of the surround rings. When the rings were ordered in a 'wedding cake' arrangement, the matching disk settings in the high-articulation condition were lower than the settings in the low-articulation condition. When rings were ordered in an 'amphitheatre' arrangement, the settings in the high-articulation condition were higher than the settings in the low-articulation condition. The results were independent of whether the disk was an increment or a decrement. Our results demonstrate that the effects of articulation depend critically on the spatial arrangement of the visual scene.

◆ **Enhancing simultaneous lightness contrast by increasing surround articulation:**

When and why it works

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It has been informally shown [Gilchrist et al, 1999 *Psychological Review* **106** 795–834; Adelson, 2000, in *The New Cognitive Neurosciences* Ed. M Gazzaniga (Cambridge, MA: MIT Press)] that simultaneous lightness contrast (SLC) is enhanced when the dark and light surrounds of the classic display are replaced by articulated fields of equivalent average luminances. We explored this effect systematically, by comparing dark and light homogeneous and articulated surrounds in all possible combinations. Relative to their surrounds, the two targets could be double increments in luminance, double decrements, or one increment and one decrement. Observers adjusted the luminance of one target to match the achromatic colour of the other. Gilchrist et al's (1999) anchoring model accounts for increased SLC on articulated surrounds by assuming that (i) SLC occurs because in the local framework (target plus immediate surround) the incremental target is white rather than grey, and (ii) increasing the articulation of such a surround causes a stronger weighting of the local framework, thus magnifying the difference between the two targets. Our results are consistent with the first but not with the second assumption, and are discussed in the light of a modified version of the anchoring model.

◆ **Contrast effects and local white distribution**

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Contrast is the well-known observation in which a gray in a white surround appears darker than in a black one. An example is a 32×32 pixel gray area subtending 1.5 deg on a black background—256 pixels on a side. The gray appears dark when surrounded by a band of white—12 pixels wide. The white band is made up of 2112 individual white pixels. If these 2112 white pixels are redistributed uniformly in the black background, the gray changes its appearance. In this distributed pattern of white pixels the gray patch looks lighter. We measured the appearance of the gray patch as influenced by 2112 white pixels in a great many different spatial configurations. The sets of different spatial patterns of white pixels that generate the same matching lightness for gray are defined as equivalent backgrounds. We then analysed the spatial properties of equivalent backgrounds, in terms of frequency, position, distance, etc. The effects of local presence of white are presented together with an analysis of the spatial properties of different intermediate surrounds in terms of changes of visual appearance.

◆ **How lightness is affected by the presence of chromatic surfaces**

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Lightness perception has been mainly studied in the achromatic domain. We started to explore how it works with achromatic and chromatic stimuli. The main question is how lightness perception works when coloured and grey surfaces are present at the same time in the visual scene. Following the concepts proposed by the anchoring theory (Gilchrist et al, 1999 *Psychological Review* **106** 795–834), we examined if the anchoring and the scaling rules, in a condition where chromatic and achromatic surfaces were interacting, worked in the same way as the one with grey surfaces only. We ran an experiment with four conditions, using five squares as target, under Gelb illumination. In the first condition there were only grey surfaces, so replicating the five-squares experiment by Cataliotti and Gilchrist (1995 *Perception & Psychophysics* **57** 125–135). In each of the other three conditions, we substituted an achromatic surface with a chromatic one of the same luminance. Equiluminance was assessed by asking subjects to detect illusory contour made by coloured and grey papers. We also found that scaling is not precise and lightness of considered surfaces is compressed, but we additionally found that scaling is affected when the yellow, replacing the white, is present in the visual scene. In another experiment, subjects have been asked to judge a black surface in three different conditions: (i) classic Gelb effect (only the black surface is present), (ii) grey surfaces (classic staircase Gelb effect), and (iii) coloured surfaces (chromatic staircase) of the same luminance as that of the grey ones. We found a significant difference among the three conditions.

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◆ **The locus of error paradigm applied to an illumination-based explanation of simultaneous lightness contrast**

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In the simultaneous lightness contrast (SLC) illusion, a gray target against a black background appears lighter than an equal gray target against a white background. Several explanations have been proposed for this illusion. Using their locus of error paradigm, Gilchrist et al (1999 *Psychological Review* **106** 795–834) found that the SLC illusion is primarily caused by a lightening of the target on the black background. Their findings were a critical blow against a simplified lateral inhibition account, and provided strong support for an anchoring theory explanation. However, this finding does not address another rival hypothesis proposed by Agostini and Galmonte (2002 *Psychonomic Bulletin & Review* **9** 264–269), who showed that the size of the SLC illusion increases when luminance gradients are placed around the two gray targets. Their hypothesis is that the larger illusion is due to the perceived illumination induced by the luminance ramps. In our study, the locus of error paradigm was used to test this hypothesis. Two stimuli were used—a standard SLC display and a modified version with luminance ramps surrounding, but not touching, the targets. Results show a much larger illusion with the modified SLC display, but only for the target on the black background, while the target on the white background does not seem affected by the presence of luminance ramps. The white target nevertheless displayed a strong glare effect (Zavagno, 1999 *Perception* **28** 835–838). This finding provides further evidence for an anchoring theory explanation of the SLC illusion.

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◆ **Interaction of luminance and texture borders in brightness perception**

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Previous studies have shown that adding a luminance border in the stimulus can block brightness spreading. We investigated the influence of the spatial range of luminance and texture borders on brightness spreading by measuring masking tuning functions for perceived brightness. The stimulus was either an incremental or a decremental circular disk (6 deg) of uniform luminance (10% contrast) on a gray background (32 cd m^{-2}). An annular mask of one octave bandpass noise was superimposed on the disk border. The mean luminance of the mask was locally the same as the mean luminance of the display. The noise centre spatial frequency was varied from 0.52 to 7.5 cycles deg^{-1} . The width of the annulus was varied in two conditions: (i) the outer diameter of the annulus was constant (8 deg) and the inner diameter was varied (3–7 deg), (ii) the inner diameter was constant (3 deg) and the outer diameter was varied (5–8 deg). The perceived brightness of the disk inside the annulus and the mask covering the disk were measured separately with the 2AFC method of constant stimuli. The masking tuning functions were band-pass (width ~ 1.5 octave, centre at ~ 2 cycles deg^{-1}), reducing the perceived brightness (darkness) of the disk. To reach the maximum effect, the mask had to extend 1 deg inwards over the disk border. The brightness of the mask matched the luminance of the disk (ie veridical mean luminance of the mask) and the brightness of the disk centre matched the luminance of the background. The results indicate that the brightness spreading stops at the mask border and the texture captures the brightness. The results suggest that the mechanism segregating textures can modulate brightness perception and might be involved in other higher-level influences on perceived brightness.

◆ **Lights, shadows, and filters: A parametric study of neon brightness spreading**

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We investigated in three separate experiments the perceived achromatic colour, transparency, and phenomenal attributes of concentric-circle neon-brightness-spreading displays. Stimuli were obtained by varying the luminances of the outer arc (OA) and inner arc (IA) of circle, while keeping the background luminance constant. In the first experiment, observers modified the luminance of an adjustable region to match the achromatic colour of the central area of the displays; additional adjustments were performed on sets of control figures without IA (subjective figures) and without OA. In the second experiment, observers judged the transparency of the central area of the displays using either numerical ratings or dichotomous judgments. In the third experiment, they used four possible categories (light, shadow, filter, opaque) to describe the appearance of the displays. Only displays with intermediate background luminance were perceived as non-transparent. Displays with intermediate IA luminance were seen as transparent filters, whereas

those with intermediate OA luminance were categorised as either lights or shadows, depending on luminance polarity. Adjustment data show that a simple contrast rule accounts well for induction effects in OA-only and IA-only figures. Data concerning complete figures show an interaction between OA and IA luminances in determining the percept; in particular, the contrast effect of OA luminance appears modulated by IA luminance in a nonmonotonic fashion. We discuss the implications of these findings on our current understanding of the mechanisms of neon brightness and colour spreading.

◆ **Perception of the direction of illumination in shaded images of convex polyhedra**

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Shading of 3-D objects is due to variations in luminance or colour as a function of the angle of the illumination direction with respect to the surface. Shading elicits a compelling sense of shape, surface, and illumination properties. However, it is not yet certain how this is achieved. We used an illuminant direction matching procedure to examine how well human observers can estimate the direction of illumination in images of rotating polyhedral shapes in different light fields. Stimuli were renderings of a dodecahedron and a sphere projected orthographically and juxtaposed on a CRT screen. Two lighting modes (collimated and hemispherical diffuse lighting), twenty-six illuminant directions (differing in azimuth and elevation), and perfectly diffuse reflectance with albedo 0.5 were used to render the faces of the two stimuli. At the start of each trial, the two stimuli were presented with different illumination directions. Observers adjusted the direction of illumination on the sphere to match the direction of illumination on the dodecahedron. Results revealed no systematic difference in matched directions between the two lighting conditions. No difference between azimuthal directions but significant differences between elevation directions were found; frontal directions were matched more precisely than rear directions. This suggests that, in the absence of cast shadow, observers may use the location of the brightest point as a cue to the direction of illumination. This is reasonable because, for Lambertian reflectance, the peak in the luminance distribution remains fixed, although the appearance of image shading can be appreciably changed under different lighting conditions.

◆ **Integration of the multiple assumptions for shape from shading**

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Humans perceive a unique shape from an image with shading, although it is impossible to reconstruct a unique shape from shading mathematically. For perceiving shape from shading, it has been claimed that humans use some assumptions, such as 'the light from above assumption', 'single light source constraint', and 'the convexity assumption' to resolve the ambiguity. In our previous research, we found that 'the smooth-shape assumption' also works. The assumption was derived from the fact that humans have a tendency to regard the whole surface of an object as smooth. It has been found that each assumption works when perceiving shape from shading, but when multiple assumptions are available at the same time and are inconsistent with each other, the perceptual outcome is not predictable. In this research, we investigated how the multiple assumptions are integrated for perceiving shape from shading. In our experiment, we used two kinds of assumptions, which are 'the light from above assumption' and 'the smooth-shape assumption'. Stimuli simulated convex or concave shape. Shapes (convex or concave) indicated by these assumptions contradicted each other in the inconsistent condition and agreed with each other in the consistent condition. Observers viewed the stimuli for 1 min and reported the perceived shape (convex or concave) of the stimulus continuously. We found that the perceived shape alternated in the inconsistent condition and was stable in the consistent condition. These results indicate that assumptions are integrated in an exclusive manner, not in an inclusive manner.

◆ **Microgenetic analysis of phenomenal transparency**

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We investigated the microgenesis of transparency perception. Two intersecting squares were used as a model for generating stimuli. The model consisted of an upper-left surface which had the shape of Γ , a bottom-right surface which had the shape of a mirror-inverted letter L, and a small square nested between Γ and L. The gray levels of these surfaces were varied, whereas the background was always black. The variation of the gray levels resulted in three patterns: T (perceived transparency), S (perceived spotlight), or M (perceived mosaic). All three patterns can be described both globally (two overlapping squares) and locally (three juxtaposed surfaces).

The primed matching paradigm was used. The test stimuli were global (two squares) or local (two Ts or two mirror-inverted Ls). There were two prime types: identical (two figures equal to test stimuli) and perceptual (T, S, and M patterns). Prime durations were 50 ms and 400 ms, and the ISI was 30 ms. Ten subjects were asked to respond whether the two figures of test stimuli are same or different. The results show no difference in reaction times between identically primed global and local test figures. However, the perceptually primed global test figures are processed significantly faster than local test figures in both prime duration conditions only for T and S patterns. These results suggest that the complex perceptual descriptions (transparency and spotlight) are generated very early in the perceptual process (50 ms).

◆ **Linear contours of occluded objects and transparency**

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The present study focused on the role of linear contours in initiating surface interpolation processes. Kanizsa [1955 *Rivista di Psicologia* 49 3–19; English version: 1979 *Organization in Vision* (New York: Praeger)] observed that linear contours can, in particular conditions, generate a phenomenal transparency. The effects have been investigated on patterns made up of two geometrical figures, one partially occluded. The linear contour of the occluded figure was visible above the occluding one, bordering the occluded shape. Observers had to indicate whether they perceived transparent surfaces and had to rate their degree of 'opacity'. The results demonstrated that a homogeneous surface can be perceived as split into two layers, a transparent film and a layer beneath, if the linear contour of the occluded shape continues above the occluding one. The phenomenon arises in conditions in which the occluded figure has a luminance intermediate between the occluding shape and the ground. The effect is enhanced when the difference in luminance between the occluding and the occluded shapes is small. Moreover, results reveal that the luminance of the linear contour is important. With luminance magnitudes close to that of the occluding shape the effects can reverse and give rise to phenomenal transparency of the occluding shape. The results are discussed in the light of the theories of transparency.

◆ **Fluorescence thresholds in a complex scene**

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The study of chromatic colour perception also includes the phenomenon of surface colour perception. In certain conditions, surfaces can take on the appearance of colour self-luminosity. Evans coined the term 'fluorence' to distinguish this type of perceptual phenomenon occurring when the luminance of an area in a more or less complex composition is much higher than that of the background from other similar phenomena produced by physical phosphorescence and fluorescence. In this study, we used the double staircase method to measure the absolute thresholds of colours so that they appear luminous in a complex scene. A coloured Mondrian, composed of rectangles of different surface colours, was generated on a computer monitor at three different levels of simulated illumination (corresponding to an average luminance of 8.57, 4.05, 1.46 cd m⁻²). One rectangle, completely surrounded by achromatic areas, was designated as the target, which appeared as either yellow, green, blue, or red, according to the methodological requirements of the chosen procedure. Fluorescence thresholds depend on the level of illumination: the lower illumination, the lower the threshold. Fluorescence thresholds for the four hues are significantly different from one another (in the order: yellow, red, green, blue) and they are lower than white luminance, except for yellow fluorescence threshold, which is higher than white luminance at the two lower illumination levels and similar to white luminance at the higher illumination level.

◆ **Functional anatomy of a cortical region sensitive to object luminosity**

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Thanks to modern imaging techniques, our knowledge about human cortical brain regions involved in the perception of visual object properties such as colour or motion has recently dramatically increased. In contrast, neural mechanisms involved in a visual distinction of self-luminous and reflecting surfaces remain largely unknown, despite their possibly distinctive role in visual attention and scene exploration. Using fMRI, we investigated in twelve healthy volunteers the brain regions involved in the perception of objects which appear to be self-luminous (sources of light) as distinct from those objects which appear to reflect light. Stimuli were cross-like figures

with luminance gradients (Zavagno, 1999 *Perception* **28** 835–838; Zavagno and Caputo, 2001 *Perception* **30** 209–222). These stimuli can be modulated so that they produce a percept of luminosity or reflectance without changes in the luminance of the stimulus area that is seen as self-luminous or reflecting. Additional stimuli controlled for effects induced by luminance gradients, and distinguished possible luminosity-sensitive regions from brain regions sensitive to changes in luminance. Data were analysed with SPM'99. A group analysis revealed luminosity-specific bilateral activation in the posterior parts of the occipito-temporal and/or collateral sulci, at the border between Brodmann areas 19 and 37. Individual analysis showed bilateral activation of this region in eight and unilateral activation in four subjects. These data suggest for the first time the existence of an occipito-temporal region that is specifically activated by self-luminous objects, that could be involved in the perceptual distinction between self-luminous and reflecting surfaces of similar luminance.

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◆ **Coexistence of colour filling-in and filling-out in segregated surfaces**

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When there is a colour/luminance gradient from the fovea to the periphery, a prolonged fixation leads to the foveal colour spreading in this direction. Against the traditional notion that colour spreading stops at a luminance border, colour in some cases spreads beyond luminance-defined gaps (Shimojo et al, 2002 *Perception* **31** Supplement, 107). Both adaptation and ambiguity in the segments due to large eccentricity are necessary. We examined the effects of size and grouping/segregation. In experiment 1, we used radial colour gradients with variable sizes of central colour area. With a small central area, filling-in of peripheral colour to the centre was observed, and with a larger central area, the direction of filling was towards the periphery (filling-out). When the same colour gradient was displayed only in small discrete patches on a black background, (i) the time required for colour filling-in was drastically reduced, and (ii) the direction of colour filling was consistently outward. In experiment 2, we introduced a second colour gradient in the background. Size of the central colour in the background was manipulated, while the colour gradient of the patches was fixed. The results indicate that when the central colour area of the background was small, filling-in occurred in the background, even as filling-out occurred in the patches. Moreover, delays between these two filling effects can be very large, up to 10 s. Together with our reports based on configuration (Wu et al, 2003, VSS03, Abstract 193) and motion (Kanai et al, 2003, VSS03, Abstract 139) as a segregation cue, the results suggest that the filling effects occur within segregated surfaces, and thus two distinctive fillings can co-occur if there are multiple surfaces formed in depth.

◆ **Dynamics of filling-in with colours**

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Peripheral targets quickly fade from view with strict fixation (Troxler, 1804 *Ophthalmologische Bibliothek* **2** 51–53) and become filled-in with the colour of the surround [see Pessoa and De Weerd, 2003 *Filling-in* (Oxford: Oxford University Press)]. In natural scenes, stimulus parts with common boundaries can be objects in front of a background or background for other objects. Thus, competition is created between several possible filling-in processes. We investigated colour filling-in with concentric disk–ring arrangements presenting blue, green, yellow, red, and grey colours in all possible combinations. Six observers participated. The central disk had a diameter of 9.1 deg, while the rings subtended 4.6 deg. Fixation was binocular. Patterns with two or three approximately equiluminant colours were used. When a middle ring of a given colour, eg blue, was placed in between, eg, a green central disk and a green outer ring, filling-in proceeded in two ways. In the majority of cases the middle ring was filled from the inside and outside simultaneously. On other occasions filling-in occurred in two steps: (i) first, the colour of the middle ring invaded the centre (ii) second, the colour of the outer ring permeated the area both of the middle and centre. Thus, filling-in occurred from the stimulus periphery to the centre. Patterns of three colours behaved similarly. However, in these stimuli the consecutive mode of filling-in occurred more often than with two colours. The filled-in colour was always the same as that of

the inducing stimulus, suggesting a lateral (long-range) process independent of a negative (local) afterimage. Red was a strong inducer, but resisted filling-in, while yellow was less effective. When the edge between centre and surround was covered by a 2 deg black annulus, the centre assumed the darkness of the occluder.

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LOW-LEVEL PROCESSES—SPATIOTEMPORAL ASPECTS

◆ Pupillary response to grating stimuli

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The pupil is thought to respond both to the amount of light and the structure of the stimulus. It also responds to the cognitive demands of a variety of tasks. The present study was motivated by a desire to understand some of the rules governing its behaviour. The pupil shows a reflex constriction when the visual input changes, even in the absence of a mean luminance change. Previous studies have emphasised the role of cortical pathways in driving this response, rather than subcortical mechanisms [Barbur, 2002, in *Visual Neurosciences* Eds L M Chalupa, J S Werner (Cambridge, MA: MIT Press)]. Thus, processing of changes in spatial structure, motion, and colour in striate areas seems to feed into the pupil-constriction mechanism. We examined how the extent of pupillary change on static, monochrome grating onset varies with stimulus contrast and spatial frequency at constant mean luminance. We conclude that the light reflex pathways are heavily involved, and that local (not global) luminance changes play a major role in determining the pupil's reflex. The local luminance increases appear to drive the fast 'light on' reflex constriction, while simultaneous local luminance decreases, elsewhere on the retina, produce a slower 'light off' re-dilation. Acting in parallel, a separate reflexive mechanism responds to high-spatial-frequency onset. In support of this, we found that avoiding local luminance increases, by preceding the grating with a high-luminance mask, minimised or even eliminated any stimulus-onset constriction. As well as contributing to our understanding of pupillary processes, these findings have implications for stimulus design to allow the use of pupillary measures of cognitive load, untainted by reflexes, in vision.

◆ Relative efficiency of Bayesian and fixed-step-size staircases in sensory threshold estimation

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Fixed-step-size (FSS) staircases have been the preferred adaptive method to estimate sensory thresholds for a long time. One of the most efficient variants for 2AFC tasks involves the use of the 3-down/1-up rule where the down step is 0.7393 times the size of the up step (García-Pérez, 1998 *Vision Research* **38** 1861–1881). Bayesian procedures are replacing FSS staircases in some contexts although their original form (Watson and Pelli, 1983 *Perception & Psychophysics* **33** 113–120; see also King-Smith et al, 1994 *Vision Research* **34** 885–912) yields estimators with sub-optimal properties in which bias and standard error covary with the true value of threshold location. Fortunately, a number of modifications can be introduced in the Bayesian procedure setup that improve its performance: the use of (i) a uniform prior, (ii) a broad symmetric likelihood function, (iii) the prior mean as the placement criterion, and (iv) the posterior mean as the final estimate. A simulation study was carried out here to compare the efficiency of this optimal Bayesian procedure and the variant of FSS staircase mentioned above. Simulations finely explored the continuum of possible real thresholds and covered a variety of psychometric functions. Preliminary results show that the Bayesian procedure requires, on average, fewer trials than the FSS staircase to provide dependable estimates with a given standard error. In particular, about 80 trials for 2AFC tasks may suffice under realistic conditions; this is nearly half the mean number of trials taken by the FSS staircase to render estimates with similar statistical properties.

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◆ Distortions of perceived orientation in crowded arrays

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The difficulty of identifying a peripheral visual stimulus in the presence of flankers is generally referred to as 'crowding'. Previous studies have shown that just noticeable differences in orientation increase with the number of flankers, but the effect of flankers on the perceived orientation

of crowded arrays is not clear. Here, observers had to identify the tilt (clockwise or anticlockwise from the vertical) of a Gabor patch flanked by two other patches 3.5° away. The Gabor patches ($3.6 \text{ cycles deg}^{-1}$) were displayed along an imaginary parafoveal circle, centred on the fixation point and 3.7° in radius. The orientation of the flankers was varied between blocks of trials. We measured the threshold, defined as the standard deviation of the psychometric function, and its bias, defined as the shift of the 50% point from the horizontal. Collinear flankers caused a greater threshold elevation than orthogonal flankers. At intermediate orientations, flankers induced a strong ‘repulsion’ bias in the reported orientation of the target. If the orientation of the flankers was near-collinear, a small ‘attraction’ bias was noted. Response biases were reliably lower when the pair of flankers was asymmetrically oriented, although thresholds were still elevated relative to collinear flankers. The biases caused by flankers are similar to those seen in the interactions between first-order and second-order cues to orientation (Morgan and Baldassi, 2000 *Vision Research* **40** 1751–1763). We discuss whether models of this kind can account for the biases seen in crowding.

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◆ Adaptation effect on perception of tilted lines

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Perceived line orientation changes during prolonged inspection time. Gibson and Radner (1937 *Journal of Experimental Psychology* **20** 453–467) attribute it to the normalisation effect (perceptually adapting line shifted towards horizontal or vertical one). Adaptation to tilted line also affects the perceived orientation of a subsequently presented line (tilt aftereffect). A few hypotheses deal with mechanisms of these adaptation phenomena (inertia of simultaneous contrast, normalisation). To this time, these phenomena are not understood. It is believed that both normalisation and tilt aftereffect result from the same adaptation processes. However, the tilt aftereffect has been investigated in greater detail than the normalisation one. Our task was to investigate the influence of line orientation on perceived tilt in the course of adaptation. Four subjects were presented with adapting stimulus consisting of 3 or 5 parallel lines 3.7° of arc in length. After initial adaptation (30 s) the test line oriented at $F_i \pm n \times 0.5^\circ$ degrees to the adapting line appeared at 5.4° of arc distance from the centre of the adapting stimulus. The integer n was chosen randomly from 0 to 10. Subjects were required to make a 2AFC judgment whether test line appeared to be tilted clockwise or anticlockwise relative to the adapting line. The inclinations of adapting lines were from -10° to 100° to vertical. The results for all subjects show that three orientations: 0° , 45° , and 90° appear to be ‘stable norms’. The lines with other orientations were perceptually tilted towards the closest of ‘norms’ in the course of prolonged inspection. The experimental results are compared with those predicted by the proposed model.

◆ The perceived contrasts of sinusoidal gratings—no contrast constancy

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When the perceived contrasts of suprathreshold luminance gratings of different spatial frequencies appear equal, their physical contrasts are also equal—a phenomenon that is often referred to as contrast constancy (Georgeson and Sullivan, 1975 *Journal of Physiology* **252** 627–656). However, this contrast constancy was found to fail when suprathreshold matches are measured for gratings whose spatial frequencies cannot be distinguished (Metha et al, 1998 *Investigative Ophthalmology & Visual Science* **39** Supplement, S424). These authors have, therefore, suggested that contrast constancy may only hold for stimuli that engage distinctly different spatial-frequency mechanisms. Here, we show that this is not the case. We measured the perceived contrast for pairs of suprathreshold gratings of visibly different spatial frequencies, using a spatial 2AFC. Starting at $4 \text{ cycles deg}^{-1}$, contrast matches were measured for neighbouring (higher and lower) spatial frequencies across the visible range. Once a grating pair was matched, this contrast was used as the reference for the next comparison. Stimuli were presented on a 21-inch Sony Trinitron monitor with a VSG 2/3 board and a 12-bit lookup table. We found that spatial frequencies with the same perceived contrast have different physical contrasts. The overall shape of the suprathreshold matches was similar, but not identical, to that of the contrast-sensitivity function. The procedure was repeated for starting contrasts of 30%, 45%, 60%, and 80% with, essentially, the same result.

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◆ **A model for effective contrast in the mesopic range**

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Our aim was to model effective contrast in the mesopic range (C_{mes}) as a function of target photopic contrast (C_p), scotopic contrast (C_s), and chromatic difference (CD), plus background luminance (L_b). We defined our measure C_{mes} as the luminance contrast $(L_t - L_b)/L_b$, where L_t is the luminance of the target, of an achromatic target perceived to have the same effective contrast as the test target. The targets were 3 deg Landolt rings presented at 7° eccentricity on a uniform background with fixed background chromaticity ($x = 0.305$, $y = 0.323$). Using a staircase procedure, five subjects obtained equivalent achromatic contrasts for a large number of test target combinations of C_p , C_s , and CD across the colour gamut of the display. Measurements were made for six values of L_b in the range 10 to $0.004 \text{ phot.cd m}^{-2}$. The dependence of C_{mes} on the test-target variables was investigated with ANOVAs, and an empirical model was developed based on the statistically significant parameters. The results highlighted individual differences in the processing of luminance increments and decrements and in the contribution of colour to C_{mes} . The results also showed that the dependence of C_{mes} on C_p , C_s , and CD varied markedly with light level. The predominant factor at the higher luminances was C_p , and C_s was the main factor at the low luminances. Surprisingly, CD made a significant contribution to C_{mes} even in the mid-to-low mesopic range. Our model for C_{mes} was a complex function of C_p , sign-dependent C_s , CD , and L_b ; neither C_p , C_s , nor CD alone were good indicators of C_{mes} . Our model shows that to describe the visual effectiveness of a target under mesopic conditions it is necessary to take account of the contribution of both the rod and the cone systems to luminance contrast, combined with a contribution from chromatic mechanisms.

◆ **Time course of the hemispheric specialisation in spatial-frequency processing**

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As suggested by the visual-spatial-frequency model of cerebral asymmetry (Grabowska and Nowicka, 1996 *Psychological Bulletin* **120** 434–449), hemispheric specialisation is a dynamic system, wherein the superiority of one hemisphere over the other could change according to cognitive constraints. We have investigated this potential dynamic as a function of temporal constraints in scene-perception framework. Participants were asked to match a test scene to a priming scene. Priming scene was always unfiltered, displayed in the central visual field. Prime display times varied from one session to the other (30 ms or 150 ms). Test scenes were low-pass filtered or high-pass filtered and were presented in the left visual field/right hemisphere (LVF/RH) or in the right visual field/left hemisphere (RVF/LH) for 100 ms. Results showed (i) the classic hemispheric specialisation for spatial-frequency processing (ie a LVF/RH superiority in low-pass filter processing and a RVF/LH superiority in high-pass filter processing) when temporal constraints were strong, and (ii) a LVF/RH advantage whatever the spatial-frequency components of the test scene when temporal constraints were reduced. This temporal dynamic of hemispheric specialisation could reflect the setting up of an inhibition process from the right to the left cortex in priming-scene processing. When temporal constraints are strong, a between-hemispheric inhibition has no time to be effective and each hemisphere is working in parallel, extracting what it can from the image in relation to its spatial-frequency aptitudes. The hypothesis of an inhibition by the magnocellular pathway is currently examined by a functional neuroimaging study.

◆ **Bars and edges: What makes a feature for human vision?**

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There have been two main approaches to feature detection in human and computer vision—luminance-based and energy-based. Bars and edges might arise from peaks of luminance and luminance gradient respectively, or bars and edges might be found at peaks of local energy, where local phases are aligned across spatial frequency. This basic issue of definition is important because it guides more detailed models and interpretations of early vision. Which approach better describes the perceived positions of elements in a 3-element contour-alignment task? We used the class of 1-D images defined by Morrone and Burr in which the amplitude spectrum is that of a (partially blurred) square wave and Fourier components in a given image have a common phase. Observers judged whether the centre element (eg $\pm 45^\circ$ phase) was to the left or right of the flanking pair (eg 0° phase). Lateral offset of the centre element was varied to

find the point of subjective alignment from the fitted psychometric function. This point shifted systematically to the left or right according to the sign of the centre phase, increasing with the degree of blur. These shifts were well predicted by the location of luminance peaks and other derivative-based features, but not by energy peaks which (by design) predicted no shift at all. These results on contour alignment agree well with earlier ones from a more explicit feature-marking task, and strongly suggest that human vision does not use local energy peaks to locate basic first-order features.

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◆ **What stops lateral interactions in pattern discrimination tasks?**

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In previous research, we demonstrated that surround patterns reduce the ability to make fine spatial discriminations on centre patterns in ways consistent with interactions among low-level mechanisms. If, however, the centre and surround are out of phase with one another, or even a tiny gap of mean luminance is introduced between centre and surround, all suppressive effects disappear. Here, we asked whether the disappearance of suppressive effects was primarily due to low-level effects (ie among spatially very localised or only among V1-like mechanisms of the same phase), or whether mechanisms of scene segregation or attention also reduced suppressive effects. We segregated centre and surround in test conditions by changing the relative mean luminance of the centre and surround. Patterns to be discriminated were two patches of near-vertical sinusoids of 3 cycles deg⁻¹, displayed in a sharp-edged 40 min of arc window that differed slightly in orientation. In control conditions, surrounds were unmodulated and of the same mean luminance as the centre pattern (either 11.2 or 19.8 cd m⁻²). A second pair of controls was run with high-luminance centres and unmodulated low-luminance surrounds, and vice versa. Performance (d') was slightly reduced from original controls when luminances did not match. In test conditions, the surround was modulated (3 cycles deg⁻¹ vertical sinusoid) around either high or low mean luminance value. All four combinations of centre and surround luminance were tested. When surrounds were modulated and of equal luminance, performance was near chance. Segregation by changes in luminance reduced the suppressive effects of modulation, although to differing degrees in different observers. We conclude that higher-level processes can modulate lateral interactions.

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◆ **Orientation-dependent spatial asymmetry of surround suppression in contrast perception**

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We investigated the spatial distribution of surround suppression in contrast perception. This has been tested only with parallel centre and surround gratings, and has been found to be uniformly distributed around the centre target. Here we have studied the spatial distribution of surround suppression in perceived contrast using both iso-oriented and orthogonal gratings. All stimuli consisted of 4 cycles deg⁻¹ sinusoidal gratings. Test stimulus centre was a 1-deg circular patch. Contrast of the vertical centre grating was 0.2. Surround consisted of two sectors of an annulus presented on opposite sides of the centre, either on top and below (end-configuration) or on the left and right sides (flank-configuration) of the centre. Sector angular width was 90 deg and surround diameter 5 deg. Surround grating contrast was 0.4 and orientation either vertical or horizontal (parallel or orthogonal to the centre). Comparison stimulus was a patch of variable contrast otherwise similar to the test centre. Perceived contrast of the test centre was measured by a method of constant stimuli and a 2AFC task. Suppression was greater with parallel than with orthogonal surround grating. With parallel surround the suppression was roughly equal in the end-configuration and flank-configuration. However, when surround orientation was orthogonal to the centre, we found that the amount of suppression depended on the position of the surround. Suppression was very weak in the end-configuration, but there was a substantial increase in suppression in the flank-configuration. This indicates that, although surround suppression is relatively uniform with parallel centre and surround gratings, there may be spatial asymmetries in surround suppression that are specific to relative orientations of the centre and surround.

◆ **Long-range spatial interactions between orientations are affected by changes in background luminance**

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The functional characteristics of the spatial regime of long-range interaction between collinear orientations are revealed at coaxial separations of 15 min of arc or more between orientations. At these separations, the contrast detection of oriented targets is facilitated by collinear orientations regardless of the contrast polarity or contrast intensity of the stimuli (Tzvetanov and Dresp, 2002 *Vision Research* **42** 2493–2498). Whether background luminance affects these facilitating long-range interactions is not known. We measured contrast thresholds for the detection of line targets separated from collinear inducing lines by a gap of about 20 min of arc as a function of the contrast polarity of the stimuli and the luminance of the background on which they were presented. The effects of dark and bright inducing lines with identical Michelson contrast were tested. Interactions between the effect of contrast polarity and the effect of background luminance on long-range spatial interactions were found. When the target line and the inducing line have the same contrast polarity, facilitating effects independent of background luminance were observed. When the target and the inducing line have opposite contrast polarity, the effects of the inducing line on the contrast detection of the target line were found to vary with background luminance. The asymmetry between effects found on dark and light backgrounds with inducing lines of equivalent Michelson contrast suggests that interactions between ON and OFF pathways influence long-range spatial interactions between orientations.

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◆ **Long-range interaction at right–left symmetrical locations across the visual hemifields**

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Visual long-range interaction has been reportedly limited in space within a few degrees. Here we report extremely long-range interaction up to 10 deg separation by locating targets at the right–left symmetrical position. Two Gabor signals (GS cue and probe, $\sigma = \lambda = 0.25^\circ$, horizontally collinear) were located at symmetrical positions across the vertical meridian with different eccentricities (0° to $\pm 5^\circ$, duration = 100 ms). Detection threshold of the GS probe was measured for each eccentricity by a 2AFC staircase method. Three conditions were tested; (i) GS cue (contrast = 0.2) was presented symmetrically to probe. (ii) GS cue was presented at a retinotopically asymmetric position shifted ± 1 deg horizontally. (iii) No cue was shown (control). Stimulus specificity was examined (a) by differing cue orientations (0 – 90°) and (b) with the use of top–bottom symmetry. Threshold decreased (facilitation) by 0.26 ± 0.05 log units (four subjects, average \pm SE) under condition (i) compared with condition (iii). No facilitation was observed under condition (ii). No facilitation was found when the cue–probe orientation differed more than 30° and no facilitation with top–bottom symmetry, indicating that the interaction is specific to retinotopy, orientation, and the vertical meridian. The results suggest an existence of ultra long-range interaction extending 10 deg which is specifically served for right–left symmetrical configuration across the vertical meridian. Since no commissural connection exists between such eccentric positions in V1, we presume that the long-range interaction is achieved through global neuronal interconnections between extrastriate cortices (ie the parietal cortex) and V1.

◆ **Under conditions of backward masking, discrimination of spatial frequency remains independent of spatial separation**

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When a subject is required to compare the spatial frequencies of two simultaneous, briefly exposed Gabor patches separated by up to 10 deg, performance is as good at large separations as when the patches are juxtaposed (Danilova and Mollon, 2003 *Perception* **32** 395–414): neither Weber fractions, nor response times increase with increasing spatial separation. This result led us to question whether the discrimination is based on the direct outputs of dedicated neural comparators at an early stage of the visual system. In an attempt to force the subject to rely on the signals of such distal comparators, we have repeated the measurements with a backward mask, which conventionally would be held to limit the duration for which the stimulus was

available for sensory processing. In the present experiments, the 100 ms presentation of the two Gabor patches was followed by a mask consisting of 30 Gabor patches located pseudo-randomly. The spatial frequencies of these masking Gabors extended over the range used in the task. The mask began on the frame following the target stimuli and stayed on the screen for 500 ms. The two Gabor patches were presented at a constant eccentricity, their centres lying on an imaginary circle of 5 deg radius which was centred on the fixation point. The spatial separation of the Gabors was varied in different blocks. The introduction of the backward mask slightly increased the Weber fractions, but performance remained independent of spatial separation. One hypothesis would be that the subject compares not the representations of the stimuli in primary spatial-frequency analysers (which will be quickly occupied by the after-coming mask), but encoded representations that remain available even when the mask is being processed.
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◆ **Contour effects in object substitution masking**

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Three experiments are presented with the aim of examining which mask properties (shape, length, number) affect object substitution masking (Enns and Di Lollo, 2000 *Trends in Cognitive Sciences* 4 345–352). In experiment 1, we tested Enns's (2002 *Psychonomic Bulletin and Review* 9 489–496) claim that mask–target shape determines substitution masking. Contrary to Enns, we find no independent effect of shape, but do find an effect of contour length: mask shapes with most of the contour proximal to the target produce the most masking. In experiment 2, we explored this effect further, and found that the distance of the mask contour from the target also affects masking, but that this is independent of the effect of contour length. In experiment 3, the number of mask elements adjacent and nonadjacent to the target contour was varied. The number of the former was found to have no effect, while the number of the latter had an effect only if the amount of local contour was small. We conclude that substitution masking shares similar properties with metacontrast masking and that it has yet to be demonstrated that higher-level re-entrant processes play a role in substitution masking (Enns and Di Lollo, 2000 *ibid*).

◆ **Investigating Glass patterns: Some temporal aspects**

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We studied the relation between the detection of in-phase flickering and the perception of circular and radial Glass patterns. Two frames were repeatedly presented. In one frame, a Glass pattern was presented, while in the other frame a mask was presented. The mask was constructed in such a way that, when the pattern was presented together with this mask, it was impossible to distinguish if a pattern was circular or radial. The subject was asked to judge if the presented pattern evoked a 'radial' or a 'circular' percept. This was done for flicker frequencies ranging from 6 Hz to 20 Hz. From the data, it appeared that, in the 9–15 Hz frequency band, the detection of the phase of the flickering dots decreased below the 75% threshold, while the impression of the Glass pattern was still above threshold. These results are discussed in the light of temporal differences between local and more global (ie geometry analysing) mechanisms.

◆ **A VEP study on visual processing of global structure in Glass patterns**

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To examine visual processing of global information, we studied characteristics of visual evoked potential (VEP) associated with global structures which are considered to activate the extrastriate cortex. Three test stimuli (concentric, radial, and parallel) were composed of random dots in which pairs of dots were placed so that the orientation of each dot pair was tangential to contours of global form for each stimulus (called Glass patterns). Control stimuli were composed of randomly oriented dot pairs. Comparison of the VEP for control and test stimuli enabled us to examine visual processing of global structure. Two types of temporal presentation modes (steady state and transient) were used. In the steady-state condition, a significantly large VEP response was obtained for the concentric pattern, whereas no large response was obtained for the radial or parallel patterns. The response to the concentric pattern decreased to noise level within the initial 2 s. Further, the response could be characterised by fast onset and slow decay. In addition, stable perception of concentric patterns continued for 3 s, comparable with the time course of the significant VEP response. In the transient condition, the responses from

200 ms onwards differed between the concentric and parallel patterns. It is suggested that the VEP to the concentric pattern from 200 ms onwards showed transient and sustained components and the time course of the sustained activity (lasting 2 s) was closely related to stable perception of concentric pattern.

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◆ **Synergy among feature domains induced by first-order and second-order object properties**

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Various studies have shown that the behaviour of early visual mechanisms can be modulated by higher-level visual functions such as object vision (eg Lee et al, 1998 *Vision Research* **38** 2429–2454). Here we compare the effects of first-order and second-order properties of texture objects on the interaction of orientation and spatial-frequency modules. In inhomogeneous Gabor fields with spread in orientation and spatial frequency, subjects detected texture objects, defined as regions of different mean in first-order parameters (orientation, spatial frequency, or both), or of only different spread of first-order parameters, but with the same mean (second order). Synergy effects, defined as detection advantage for texture objects with variation of both first-order parameters (compared to variation of only one) were stronger than predicted from the assumption of independent modules for orientation and spatial frequency, and were found for objects defined by first-order and second-order properties. However, when texture objects were defined by first-order and second-order properties simultaneously, there was no longer a significant increase in detection performance. Our results indicate that first-order and second-order properties are processed at independent stages, but both can combine information from different first-order feature pathways in order to enhance the detectability of objects.

◆ **Object-based synergy of modules for orientation and spatial frequency**

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Traditional theories propose that elementary features are handled in independent neural pathways at the first stages of processing (eg Treisman and Gelade, 1980 *Cognitive Psychology* **12** 97–136). However, there is growing evidence that feature modules interact even in preattentive vision (Kubovy et al, 1999 *Psychonomic Bulletin and Review* **6** 183–203). It has been shown that the firing rates of V1 cells of awake monkeys increase after 80 ms if the activity is part of signalling figure but not of ground (Zipser et al, 1996 *Journal of Neuroscience* **16** 7376–7389). Therefore we addressed the question whether the presence of texture figures affects how features from different domains interact. In the experiment, subjects detected texture figures in homogeneous Gabor fields. Figures were defined by contrast in (a) spatial frequency, (b) orientation, or (c) both features (feature conjunctions). The increase in detection performance for feature conjunctions compared to single features was significantly better than predicted from the assumption of independent feature modules when the texture figures had rectangular or square shape. When figures degraded to one-dimensional Gabor element arrays, the synergy effect for feature conjunctions vanished. Further, the strength of feature synergy was independent of the overall figure salience. Our results indicate that synergy of orientation and spatial frequency modules is modulated by the presence of objects.

◆ **Surface-slant judgment from texture and motion**

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We have previously observed systematic differences in slant perception by means of probe adjustment for different types of synthetic texture (Rosas et al, 2002 *Perception* **31** Supplement, 27). These results led to a rank-order of textures according to the correlation between the depicted and perceived slants, when a particular texture was mapped on the surface. Textures composed of circles tended to allow the best slant judgments, followed by a leopard-skin-like pattern, then by a 'coherent' noise, and finally a fractal noise inducing the worst performance. Here we compare those results with an experiment in which subjects were asked to judge the slant of textured flat planes that could have two types of motion: translation of the planes in the vertical direction (parallel to the viewing direction) and horizontal direction (orthogonal to the viewing direction). Our results show that the performance in most cases was better for the moving planes than the performance for static planes, for all types of textures and both types of motion. The perceived slant of the moving planes was comparable for both types of motion.

A simple summation of cue information would predict a similar enhancement of performance for all types of texture, which was not observed. A cue combination in which the influence of a particular cue is related to its reliability, such as the modified weak fusion model (Landy et al, 1995 *Vision Research* **35** 389–412), would predict different influences of the texture types on the combined perception following the rank-order mentioned previously. We did not observe such gradual enhancement of performance, though the largest performance enhancement was observed for the least reliable texture.

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◆ **Texture orientation contrast across a subjective contour aids detection, but not discrimination of boundary orientation**

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Neuronal activity in V1 is modulated by nearby orientation contrast, either a single pop-out element or a boundary defined by many local orientation contrasts. In comparison, subjective contours defined by aligned line-terminations cause modulation of activity in V2 but only very weak modulation in V1. These modulations in orientation-tuned cells are caused by the integrated contour, not just a single line-termination. Combinations of mapping techniques suggest that modulation by subjective contours may be due to feedback from higher cortical areas rather than originating in V1 or V2. In the present study, we used a speed–accuracy trade-off paradigm to investigate the temporal dynamics of texture border processing. The texture stimulus was composed of randomly placed, uniformly oriented line segments. A discontinuity was defined by either a boundary of aligned line terminations (subjective contour), or with an additional change in orientation across the boundary (orientation contrast). In a detection task, subjects indicated whether the boundary appeared to the left or right of fixation, and in an orientation-discrimination task whether the boundary tilted clockwise or anticlockwise. Detection of contours with orientation contrast was maximal at all response times and eccentricities. Detection of subjective contours was slower and asymptoted at a lower accuracy as eccentricity was increased. After correction for lower detection rates, we found that discrimination performance for subjective contours was not significantly different from that for contours with orientation contrast. We conclude that while orientation contrast is a powerful cue for detection, boundary integration occurs at a later processing stage in common with that for subjective contours.

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◆ **Effects of priming in texture segmentation**

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This study aimed at establishing whether, as follows from the perceptual representation system (PRS) hypothesis, mechanisms for coding configural properties in texture segmentation are similar in perception and short-term perceptual memory (STPM). We investigated whether implicit STPM for a texture bar oriented 45° clockwise or counterclockwise produced different priming effects on texture segmentation, depending on whether bar orientation was parallel or orthogonal to its line texture elements. Orientation discrimination in the first block was at threshold (74%) for parallel but not for orthogonal (40%) bars. Training brought all performances to ceiling, suggesting that training makes parallel and orthogonal bars equally salient. However, performance was worse when the stimulus in the n th trial was preceded by a parallel bar rather than an orthogonal one, regardless of whether the bar in the n th trial was parallel or orthogonal; this (priming effect) decreased with training. These results indicate that in the first trials the parallel, more salient, bar is coded in the PRS by low-spatial-frequency mechanisms selective to the whole-bar orientation, and that this STPM may interfere with local texture segmentation. On the other hand, the orthogonal, less salient, bar is coded in the PRS by high-spatial-frequency channels selective for texture elements or texture borders and interferes less with texture processing. Learning equates salience of parallel and orthogonal bars so that the memory code, as well as the sensory processing, become similar for the two kinds of texture. These findings support the view of a common mechanism (namely, PRS) responsible for visual processing and STPM of visual stimuli, which operate at early levels of the visual stream.

◆ **Twinkle time: The effects of temporal flicker rate upon judgments of relative durations**

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Recently, it has been shown that prior exposure to temporal flicker can influence perceived duration. We explored the possibility that duration perception can be influenced concurrently. Observers judged the relative durations of successive periods of temporal flicker. We used fields of limited-lifetime dots to create temporal flicker and manipulated the lifespan of the dots to determine the rate of the flicker. The perceived durations of test periods ($500 \text{ ms} \pm 240 \text{ ms}$) were contrasted with standard periods (500 ms of $10 \text{ lifetimes s}^{-1}$ flicker). Order of presentation was randomised. We found that test periods containing relatively fast rates of flicker (40 and $20 \text{ lifetimes s}^{-1}$) seemed relatively long whereas slow rates (5 and $2.5 \text{ lifetimes s}^{-1}$) seemed relatively brief. Using a centre-surround configuration, we could also distort the perceived durations of periods of centrally placed flicker of $10 \text{ lifetimes s}^{-1}$. When temporally and spatially surrounded by relatively rapid flicker ($20 \text{ lifetimes s}^{-1}$), the perceived durations were relatively long, and brief if surrounded by a slow rate ($5 \text{ lifetimes s}^{-1}$). To some extent, this influence was spatially specific. If the test periods were physically displaced from the inducing flicker, distortions of apparent duration were mitigated. These findings are inconsistent with contemporary accounts of time perception as they suggest the existence of spatially specific timing mechanisms.

◆ **Event-related cortical potentials correlated with behavioural performances in a duration discrimination task**

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A behavioural and event-related potential (ERP) evaluation was undertaken for the purpose of understanding the role of prefrontal and cortical regions previously suggested to play a role in temporal discrimination [Casini et al, 1999 *Journal of Psychophysiology* **13**(2) 117–125; Monfort et al, 2000 *Neuroscience Letters* **186**(2) 91–94; Paul et al, 2003 *International Journal of Clinical Neurophysiology* (submitted)]. Our hypothesis is that these structures are implicated in memory and decision processes responsible for behavioural performances. Stimulus pairs of durations lasting between 100 ms and 1200 ms were presented in three different orders and subjects were asked to estimate whether the second duration was longer or shorter than or equal to the first. ERPs were recorded during the entire length of stimulus pairs in a 32-electrode array. The results show that a contingent negative variation (CNV) was observed between and during duration presentations, as well as a long positive component (LPC) just after their presentation. Correlational analyses show that the amplitude of the frontal and prefrontal positive component was tightly correlated with behavioural performances only with long ($> 500 \text{ ms}$) stimulus durations. This result was not found with the CNV. These results may indicate that the slow positive frontal and prefrontal wave reflects decision processes, whereas the CNV reflects memory functions. There is a clear implication that prefrontal and frontal cortical regions play a determining role in the treatment of lengthy intervals.

◆ **The lateral effect of a luminance-modulated annulus on a foveal afterimage assessed by a compensation method**

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Last year we reported that the appearance of a foveal afterimage could be influenced by luminance changes in the surround. A flash-induced afterimage on a grey central disk of 8 deg radius undergoes changes in brightness and size when a surrounding annulus is modulated in luminance at 0.75 Hz . The afterimage becomes darker and smaller when the annulus is bright and becomes brighter and larger when the annulus is dark. Thus, it behaves as if the central background disk were modulated in the same phase as the annulus. Simultaneous contrast may be ruled out as a causal factor because it would predict the opposite behaviour of the afterimage. The same applies to luminance changes on the disk produced by size variations of the pupil. To find out whether light scatter from the ring could cause the pulsation of the afterimage, we calculated for each subject the amount of interocular stray light in the experimental condition and compared it to the background modulation required for a comparable change in afterimage appearance. We found that the afterimage pulsation persists even when the foveal stray light from the annulus is compensated for by a counterphase luminance modulation of the central disk. In view of these

results, we propose that the afterimage pulsation originates from the luminance modulation of the annulus, in part through a long-range lateral effect.

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◆ **Offset signals of visual object trigger perceptual fading**

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After prolonged fixation, a stationary object placed in the periphery fades and disappears from our visual awareness (the Troxler effect). Previously, we have shown that such fading is triggered, in a time-locked manner, by visual transients such as additional visual stimuli flashed near the object, apparent motion, and a brief disappearance of the object itself [Kanai and Kamitani, 2003 *Journal of Cognitive Neuroscience* 15(5)]. Because each of these stimuli contains both onset and offset components, we further explored whether the onset or offset transient is critical for the fading induction. We used five stimulus conditions to dissociate their effects. In all the conditions, the target object (a red disk on a near-isoluminant green background) was continuously present for the entire trial (2082 ms). (1) A white ring was flashed for 118 ms in the middle of the trial (flash condition). (2) A white ring appeared in the middle of the trial and remained on until the end (onset condition). (3) A white ring was present from the beginning of the trial and disappeared in the middle of the trial (offset condition). (4) No ring was presented (control condition A). (5) Both the target disk and the ring were presented continuously for the full duration of the trial (control condition B). Fading was induced only in the flash condition and the offset condition, and the strength of the effect did not differ between these two conditions. The onset condition did not induce a larger fading effect than the control conditions. These results indicate that the critical factor for the transient-induced perceptual fading is the offset signal of an object. Such offset signals may provide a reset signal for the visual system and facilitate the processing of subsequent stimuli.

◆ **Visual reaction time to second-order stimuli**

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Reaction time (RT) to onset detection of sinusoidal gratings increases with increasing spatial frequency and could be explained by the competition between two separate (transient and sustained) first-order temporal mechanisms. Recent measurements of the temporal properties of second-order vision have suggested that the impulse response to contrast-modulated noise was sustained and was similar to the response to sinusoidal gratings in noise (Schofield and Georgeson, 2000 *Vision Research* 40 2475–2487). The above results raised the question about the processing speed of second-order vision compared to that of first-order vision. Here we measure visual RTs for three types of stimuli displayed with equal rms contrast, varying in spatial frequency (ranging from 0.5 to 8 cycles deg^{-1} in steps of $\frac{1}{2}$ octave): sinusoidal gratings alone (L), sinusoidal gratings added to pseudo dynamic visual noise (LM), and sinusoidal contrast modulations of a pseudo dynamic noise (CM, second-order stimuli). Data from simple RT experiments show that: (a) RT increased with increasing spatial frequency of luminance gratings (L and LM) or CM stimuli; (b) at the same spatial frequency, RT for second-order stimuli was larger than RT for sinusoidal gratings alone and LM stimuli; and (c) the shape of three RT curves (L, LM, CM) was very similar and slightly non-monotonic. This suggests that, although second-order vision is somewhat slower than first-order vision, the performance of both visual mechanisms to detect the stimulus onset seems similar.

◆ **Exploring alternatives in contrast—contrast phenomena**

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Modulatory effects of a surround on apparent contrast of the centre have been explained by lateral interactions among early cortical neurons or by summation within large receptive fields with antagonistic regions that differ in spatial extent. We attempted to psychophysically distinguish between these alternatives. Test stimuli were horizontal sinusoidal gratings (8 cycles deg^{-1}), with equal contrasts (0.25), presented in a circular disk or in an annular configuration. To define the extent of a perceptual contrast summation field, we first measured the apparent contrast of a circular test patch by matching the apparent contrast of a test patch of varying diameter (0.25–2 deg) to a 1 deg comparison patch. As the diameter of the test patch increased, apparent

contrast first increased, then decreased at diameters larger than 0.5 deg. We took this turning point (0.5 deg) as the size of perceptual summation field of apparent contrast. In a second experiment, we matched the contrast of an annular stimulus with a 1.0 deg outer diameter and variable (0–0.75 deg) inner diameter using a variable-contrast 0.5 deg circular patch as a comparison. The centre of the annulus test ring was either unmodulated or had the same-frequency grating as the annulus, either in same or orthogonal orientation. Relative to the apparent contrast of the optimal disk (0.5 deg), the annulus contrast with an unmodulated centre was suppressed approximately 15%, regardless of its inner diameter (except when it was 0). Less suppression was found when an orthogonal grating was added, and minimal or no suppression was found with the same-orientation centre. These results are more easily explained by a large-receptive-field model with overlapping inhibitory and excitatory regions.

◆ **New results of modelling of the dynamic processes in the human visual system**

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We report here some new results obtained following an improvement of the model of the human visual system developed by us earlier (Krasilnikov et al, 1999 *Journal of Optical Technology* 1 3–10). We described and explained there the mechanism of dynamic processes taking place in the human visual system. Mathematical modelling of the visual system under dynamic conditions with observation of achromatic noisy images indicated that, by taking account of the inertia of the visual system and of the delay of inhibitory signals with reference to the excitatory, we can establish the main fundamental laws of the human visual system and its dynamic characteristics. Using our new model we derived mathematically (i) quite a number of well-known psychophysical laws, such as Bloch's, Pieron's, Blondel–Rey's, Bunsen–Roscoe's, etc; (ii) formulas for calculating the spatial and temporal contrast-frequency characteristics of the visual system; (iii) formulas for calculating the dependence of threshold amplitude of the retinal illuminance change upon a flicker frequency; and (iv) formulas for the efficiency of the human visual system as a function of duration of presentation of a moving object in a noisy image. Comparison of the obtained results with experimental data demonstrated good coincidence. Moreover, the model enables us to predict if the perceived sharpness of the edges of the moving object is higher or lower than when the object is stationary, for different values of speed of the object and for different values of sharpness of its static analogue.

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FROM NEURONS TO PHENOMENOLOGY

◆ **Chaotic trend in insect electroretinogram**

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Visual system dynamics was investigated by means of an electroretinographic (ERG) signal, recorded for three different levels of intermittent light intensity. Semi-quantitative tests based on the chaos theory were applied to approach the degree of complexity in *Drosophila melanogaster* visual system, for both raw and smoothed ERG signals. Lyapunov exponent, fractal dimension, and correlation time were calculated for original data series as well as for those obtained after dominant-frequency-signal extraction. The correlation time was slightly increased after signal smoothing, leading to slight enhancement of signal predictability while fractal dimension was decreased. Dominant quasi-periodic dynamics were found to overlap a chaotic trend which is more evident in low-intensity light, when the amplitude of ERG signal generated in the neural cell from lamina ganglionaris is higher.

◆ **Quantitative analysis of feedforward and feedback connections of cortical areas 17, 18, 19, and 21a in the cat**

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In the process of visual recognition, the comparison of external sensory information with internal mental information takes place. About 30 cortical areas are involved in this process. Intrinsic, feedforward, and feedback connections of single cortical columns of areas 17, 18, 19, or 21a in the cat were investigated. We made microiontophoretic injections of horseradish peroxidase and estimated the number of retrogradely labelled cells in different cortical areas and lateral geniculate nucleus. We converted the extent of labelled cortex in millimetres into a span in degrees of

visual field. Projections from all areas are centred at similar retinotopic locations as the injected column. Cortical columns of four investigated areas receive much higher number of feedforward projections compared to the number of feedback projections. The number of feedforward projections from areas 17 and 18 to areas 19 and 21a was comparable to the number of their intrinsic connections. There was a difference in areas of origin of feedback projections to areas 17 and 18, and to areas 19 and 21a. Quantitative data on feedback connections of single cortical columns are presented and their significance for visual information processing is discussed.

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◆ **Visual imagery activates spatially specific representations in human V1**

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To what extent does visual imagery reflect our internal view of perceptual objects, and does it result from the top-down activation of representations used for visual perception? Controversy surrounds whether primary visual cortex (V1) is involved in visual imagery and whether early visual areas represent the spatial attributes of imagery. To address these issues, fMRI was used to investigate the spatial specificity of imagery representations in retinotopically defined visual areas. Subjects received alternate physical stimulation and visual imagery trials in each fMRI scan. On stimulus trials, a flickering checkerboard (size 4 deg, temporal frequency 8 Hz, contrast 50%) was presented 6 deg to the left or right of central fixation. On imagery trials, only a central cue was presented to instruct subjects to imagine seeing the flickering checkerboard in the left or right location. fMRI data were aligned to retinotopic maps collected in a separate session with Brain Voyager software. Visual imagery led to spatially specific activations in contralateral regions of V1 and extrastriate areas V2–V4 that were about half as large as those evoked by physical stimulation. Activation maps further revealed that precisely the same regions of V1 were active during imagery and visual perception. The spatial specificity of these imagery effects rule out the possibility that confounding factors of cognitive load or eye movements might account for these retinotopic activations. These findings indicate that visual imagery engages the same network of early visual areas as those involved in perception, including primary visual cortex. Moreover, the mechanism underlying imagery is retinotopically specific, suggesting that the spatial representation of visual imagery is likely to be veridical.

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◆ **Fisher information as a tuning parameter for stochastic resonance-based neural systems**

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Stochastic resonance is a phenomenon whereby nonlinear systems subject to noise exhibit an increment of their sensitivity to weak input signals. This general phenomenon has already been studied theoretically and experimentally in multidisciplinary contexts. For threshold-based elements arising in neural systems (Greenwood et al, 2000 *Physical Review Letters* **84** 4773–4776; Hennig et al, 2002 *Neurocomputing* **44–46** 115–120), it has been observed that for a given threshold there exists an optimum noise level that maximises the system sensitivity and, conversely, for a given noise level there exists an optimum threshold. To always work in an optimal detection regime, neural systems should continuously adapt either their internal noise levels or their threshold levels to changes of the input-signal characteristics. To be relevant to neural systems, this adaptation should be based on parameters that can be estimated locally (ideally at the level of individual neurons). Recent contributions focus attention on the use of the signal-to-noise ratio or the just-noticeable-difference in output (Wenning and Obermayer, 2002 *Neurocomputing* **44–46** 225–231). We show that Fisher information (and the associated Cramer–Rao bound) characterising the quality of the output-signal estimator is a relevant local quantity allowing neurons to optimally respond to changes in input characteristics. This approach theoretically proposed by Hongler and de Meneses (2003 *IEEE Transactions on Pattern Analysis and Machine Intelligence* in press) has now been successfully tested on actual vision systems subject to vibrations (microsaccades), working on a contrast-extraction task. Results show that threshold-based neurons can indeed be optimally self-tuned by using the Fisher information delivered by the underlying estimators.

◆ Are neural correlates of visual consciousness retinotopic?

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Does each specialised brain area contain multiple, dissociable perceptual circuits—one for each region of visual space—or in perception related to diffuse activation of a specialised area? We have set out to answer this question by studying brain activity during a visual threshold task presented at central and peripheral visual field locations. At threshold, the same stimulus is seen on some trials and not on others with the response to not-seen trials reflecting non-conscious sensory processing or preparatory attention. Any increment in this response for seen trials is a neural correlate of perception (Pins and ffytche, 2003 *Cerebral Cortex* **13** 461–474). We performed the threshold task in eleven psychophysically trained subjects, using fMRI to record brain activity at the occipital polar and medial calcarine regions mapping the central and peripheral stimuli. Our results provided compelling evidence for a retinotopic organisation of perceptual correlates. In the peripheral field experiment, perceptual activity was localised to the left medial calcarine region; in the central field experiment it was found bilaterally at the occipital pole. It seems that when we see a contour at a particular spatial location, the activity underlying the ‘seeing’ is tied to the representation of that spatial location. In searching for neural correlates of consciousness, the cells or circuits we should be looking for are those that co-localise with afferent sensory processing and activate independently for different regions of visual space. [Supported by the Wellcome Trust.]

NATURAL SCENES

◆ Performing a naturalistic visual task when the spatial structure of colour in natural scenes is changed

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A previous study (Párraga et al, 2000 *Current Biology* **10** 35–38) demonstrated psychophysically that the human visual system is optimised for processing the spatial information in natural achromatic images. This time we ask whether there is a similar optimisation to the chromatic properties of natural scenes. To do this, a calibrated, 24-bit digital colour morph sequence was produced where the image of a lemon was transformed into the image of a red pepper in small (2.5%) steps on a fixed background of green leaves. Each pixel of the image was then converted to the triplet of L, M, and S human cone responses and transformed into a luminance ($L = L + M$) and two chromatic $[(L-M)/L]$ and $[(L-S)/L]$ representations. The luminance and the $(L-M)/L$ chromatic plane were Fourier-transformed and their amplitude slopes were independently modified to either increase (blurring) or decrease (whitening) them in fixed steps. Recombination of the luminance and chromatic representations produced 49 different morph sequences, each one with its characteristic luminance and L–M chromatic amplitude slope. Psychophysical experiments were conducted in each of the 49 sequences, measuring observers’ ability to discriminate between a morphed version of the fruit and the original one. A control condition was the same task with only monochrome information. We found that colour information appeared to ‘dominate’ the results, except that performance was significantly impaired when the colour information in the images was high-pass filtered. This is in keeping with the idea that colour information is most useful at low spatial frequencies, as expected from the contrast sensitivity function for isoluminant gratings.

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◆ Local contrasts in natural images—the effect of eye movements

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The distribution of contrasts in natural images as seen by primates has previously been estimated by Tadmor and Tolhurst (2000 *Vision Research* **40** 3145–3157). They used modified difference of Gaussians as contrast operators to determine the range of contrasts that primate retinal ganglion cells and LGN neurons encounter in natural scenes. However, they did not take the effects of eye movements into account, which may change the distribution of calculated contrasts. The eye movements of twelve subjects were measured when they viewed a set of 70 calibrated natural images (grey scale, 8-bit, 1024 × 768 pixels; van Hateren and van der Schaaf, 1998 *Proceedings*

of the Royal Society of London, Series B **265** 359–366). The images were presented for 5 s each on a 21 inch monitor (frame rate 120 Hz). The display was linearised to 14 bits with a VSG 2/5. Eye positions were recorded at 60 Hz with a Pan/Tilt eye tracker (ASL, model 504) and analysed offline to yield a set of fixations for each subject and image. We have found that the distribution of local contrasts at fixated positions differs markedly from the previous estimate of local contrasts; fixated positions had more high-contrast values than previously predicted by the distribution of contrasts in natural scenes. Thus, any realistic estimate of the contrasts that constitute our visual diet must take eye movements into account.

◆ **Glare effect on spatial-frequency processing**

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The visual system analyses scenes through a series of spatial-frequency-tuned channels. Consequently, visual perception is frequently assessed by measuring contrast sensitivity as a function of spatial frequency, the so-called contrast sensitivity function (CSF). Visual impairment due to glare mainly decreases contrast sensitivity in the low spatial-frequency spectrum (Roumes et al, 2001 *Perception* **30** Supplement, 81). But these results come from elementary visual tasks such as detection of simple forms on a homogeneous background. How are higher-order spatial-frequency mechanisms disrupted by glare? Glare effect on simple form detection and on object recognition were compared. CSF was determined by using five bandpass stimuli with a two-dimensional difference-of-Gaussian luminance profile (0.8 to 12.8 cycles deg⁻¹). This was the 'simple' task. The complex task concerned the recognition of objects in a natural scene. In the latter case, two kinds of images could be displayed: 'single images' with a bandpass spatial-frequency content and 'combined images' created by the combination of two 'single images'. Two glare levels were tested. With regard to images with a restricted spatial-frequency spectrum, results showed that the main effect of the strongest glare occurred at the optimum of performance whatever the task (0.8 cycle deg⁻¹ for CSF and 3.2 cycles deg⁻¹ for object recognition). Within the recognition task, the weakest glare had no effect on performances with 'single images'; a wider spatial-frequency spectrum (ie 'combined images') was necessary to highlight the glare effect. These results are discussed in terms of method of glare effect assessment.

◆ **On change blindness in natural scenes: Towards a direct comparison of static and dynamic conditions**

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Change blindness can be produced with both static and dynamic visual environments. However, a direct comparison of these conditions has not yet been satisfactorily realised. We approached the task with the help of a new method—the video-supported spatial simulation which is normally used by architects for developing and illustration purposes. In our experiment, a computer-controlled endoscope video camera moved through a reduced-scale model (1 : 100) of an urban street scenario simulating the viewpoint of a van driver moving at a constant speed of 36 km h⁻¹. In the controlled laboratory setting we were able to repeatedly produce identical video clips of the same scenes. After shooting the initial clip, the same clip was shot again. However, this time a target object was added to or withdrawn from the scene. The two clips were digitally edited and merged into one single clip, where a sudden change occurs in absence of change-indicating 'cuts'. Twelve subjects were asked to report changes in the scenes of 336 realistic self-motion video clips (16 s each). Randomly distributed yellow cubes (perceived as lying on the street and having an edge size of about 50 cm) were used as targets and distractors. Change conditions consisted of either the appearance or disappearance of one cube during 40 ms (simulating a saccade), 160 ms (simulating an eye blink), or 320 ms blank screen intervals as well as during a non-occluded control condition. In order to avoid guessing, catch trials were introduced in all blank conditions. Corresponding screen shots of the video clips were used as the static environments. The extent of change blindness found in this study was consistently higher in the dynamic visual environments and relatively constant at all blank durations.

◆ **In which of two scenes is the animal? Ultra-rapid visual processing demonstrated with saccadic eye movements**

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The processing required to decide whether a briefly flashed natural scene contains an animal can be achieved in 150 ms as demonstrated by event-related potentials (Thorpe et al, 1996 *Nature* **381** 520–522). Recently, it was shown that this kind of decision can be performed in parallel when the subjects have to respond to one or two images presented in the near periphery (Rousselet et al, 2002 *Nature Neuroscience* **5** 629–630). All our previous studies used a go/no-go paradigm with a manual button release, the earliest reaction times typically occurring at around 250 ms. Here we report that, if saccadic eye movements are used to indicate which of two scenes contains an animal, responses are much faster. On each trial, two natural scenes were flashed for 20 ms on either side of fixation, only one of which contained an animal. The fixation point disappeared and two fixation marks were presented in order to indicate the two possible saccade landing positions. The task was to make a saccade as fast as possible to the side where the animal had appeared. Performance was remarkably good with saccadic reaction times that could be extremely short. In the fastest subjects, reliable saccades were initiated less than 160 ms after stimulus onset. It is likely that these faster responses are due to both the shorter path length in the oculomotor system and the change from a go/no-go task to one in which a target is always present. Nevertheless, the results indicate that the neural mechanisms underlying object detection must be highly automatic and even faster than was previously thought.

◆ **The spatial extent of centre – surround suppression for complex stimuli**

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Natural images have a characteristic second-order statistic since their average amplitude spectra fall with spatial frequency, f , as $1/f^\alpha$, where $\alpha \sim 1.0$. Previously, we have shown that the perceived contrast of a small central texture patch (1 deg \times 1 deg) is suppressed when it is surrounded by natural images (4 deg \times 4 deg) of varying α values and that this suppression is maximal around the α value of 1.0. Here we explored the spatial extent of this suppression. Stimulus images consisted of a central texture patch (1 deg \times 1 deg) centred on a background image. Images were either photographs or were derived from random luminance patterns (256 grey levels), all filtered to different α values. Stimuli were presented on a 21-inch monitor (120 Hz) with a VSG graphics board. Contrast suppression was measured by means of a nulling paradigm. First, we determined the α at which maximal suppression occurred using four different surround sizes (1.5 deg \times 1.5 deg to 8 deg \times 8 deg). Suppression of the perceived central patch contrast increased with surround size but maximal suppression always occurred with surrounds of α of 1.0. Thus, the tuning to an $\alpha = 1.0$ appears to be scale-invariant at those surround sizes. Next, we measured, for an α of 1.0, the spatial configuration of this suppression using surround stimuli of different area and of equal area but with different separation from the centre. We found that, for surrounds with the characteristic statistic of natural scenes (ie $\alpha = 1.0$), the suppressive region is predominantly localised to 0.4 deg from the edge of the central patch.

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◆ **Natural scene statistics and the nonlinear and extra-classical properties of cortical receptive fields**

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The extra-classical surrounds of receptive fields yield highly nonlinear effects not explainable within the classical linear-filter paradigm. We studied these effects from two perspectives. In the first approach, we used a nonlinear multi-layer architecture which consisted of linear filter mechanisms and simple ON/OFF nonlinearities. The filter mechanisms in each layer were learned (PCA, ICA) to yield an optimal adaptation to the statistical properties of natural scenes. The resulting nonlinear processing properties were then compared with recent neurophysiological data on extra-classical properties. As a second approach we used nonlinear models based on Volterra–Wiener theory and generalised measures from differential geometry. Here, the basic nonlinear interactions are AND-like (multiplicative) and the nonlinear combinations are adapted to yield a higher-order whitening of the polyspectra of natural images. We show that both types of nonlinear architectures can capture basic extra-classical properties, like surround suppression

effects, and we reveal the existence of equivalence classes in which one and the same input–output behaviour can be obtained by models which differ apparently substantially in their structure. From a theoretical perspective, the concept of AND-like combinations of spatial-frequency components is an attractive and general nonlinear extension of the classical linear-spatial-filter paradigm (it comprises, for example, all linear–nonlinear–linear schemes with squaring rectifiers). Explicit neural AND operations yield a somewhat more general class than nonlinear surround inhibition schemes, since they enable a higher sensitivity, and they can describe the components of intracellular recordings, and the observed complicated disinhibition effects.
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◆ **On measuring the ecological validity of local figure – ground cues**

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The significance of figure – ground organisation was first emphasised by Rubin [1921 *Synsoplevede Figurer* (Copenhagen: Gyldendalske)] who noted that size and surroundedness affect the likelihood that a surface is seen as figural. Stimuli designed by Kanizsa and Gerbino [1976, in *Vision and Artifact* Ed. M Henle (New York: Springer) pp 25–32] and Vecera et al (2002 *Journal of Experimental Psychology: General* **131** 194–205) pointed respectively to the role of convexity and lower-region as cues. We expect that Gestalt laws make sense because they reflect the statistics of the natural world. If figural regions tend to be convex, the visual system can evolve to exploit that fact. Using annotated natural images, we are able to characterise ecological validity by directly measuring the frequency with which figural regions are smaller, below, and more convex than ground regions. We employed a set of 100 images that have each been hand-segmented into 5 to 30 disjoint regions corresponding to objects and surfaces. Each pair of abutting segments shared a contour. Subjects were shown an image and asked to identify which segment the contour ‘belongs to’. We sampled 1200 boundary points from each image. The two segments associated with each boundary point were intersected with a local analysis window. Size was given by the number of pixels from each segment in the window. Lower-region was measured by the extent a vector normal to each segment boundary pointed upwards. Convexity was computed as the percentage of straight lines connecting point pairs in a segment that did not intersect the boundary. For each cue, we computed the logarithm of the ratio between the figure and ground measurements. We found that figural regions tended to be smaller, more convex, and occur below ground regions. The empirical distributions of feature ratios had a skewness of 0.52 for size, 0.29 for convexity, and 0.34 for lower region.

◆ **Neuronal basis of coding natural textures in area V4 of the awake monkey**

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Although objects in a visual scene are in three dimensions (3-D), it is possible to identify them on the basis of 2-D pictures. It is therefore obvious that the cues in static monocular pictures can be used for the recognition of 3-D shapes. Among these monocular cues, the texture of objects is an important source of information. Our study aimed to reveal coding specificities of natural textures by area V4 neurons in the awake macaque monkey. We trained a monkey to fixate a point on a screen during the presentation of a natural texture picture in the receptive field of a neuron. In each trial, the picture is chosen among a set of 12 textures lit under 3 different directions (36 stimuli) and their respective 36 controls (random Fourier phase). These stimuli come from the CURET (Columbia–Utrecht reflectance and texture) database. We tested 90 neurons with the 72 stimuli. 81% of the neurons have a selective response to the textures and 70% to illumination direction. A multi-dimensional scaling analysis shows that there may be clusters of neuronal responses related to a limited number of natural texture parameters. Whereas luminance or contrast cannot explain the selectivity of the whole population of cells, spatial parameters extracted from a pyramid of filters account for the clustering of some neuronal responses. These results show that V4 neurons participate in the coding of natural textures by extracting spatial parameters.

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FACE PERCEPTION

◆ Infants' face perception tested with symmetrical patterns

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Our aim was to clarify the important physical variables for face perception by infants. We investigated the symmetrical pattern of the face. In infants' face studies, Rhodes et al (2002 *Perception* 31 315–321) showed that infants preferred the less symmetrical face to the symmetrical one. In order to establish this novel preference for the less symmetrical face, infants should habituate to the symmetrical face pattern. Infants' pattern perception studies support this conclusion. Humphrey and Humphrey (1989 *Canadian Journal of Psychology* 43 165–182) showed that 4-month-old infants habituate to a vertical symmetrical pattern more quickly than to a vertical asymmetrical pattern. This suggested that 4-month-old infants have already habituated to the symmetrical pattern. Generally, face consists of a symmetrical pattern of each feature. If face perception is based on the same process of symmetrical pattern perception, decreasing the symmetrical pattern of the face would have an effect on infants' habituation time. In our experiment, three different patterns were shown to seventy infants aged 3 to 7 months: (i) symmetrical face pattern; (ii) asymmetrical non-face pattern; (iii) symmetrical non-face pattern. We compared infants' habituation to these three patterns. Results showed that, except for 3-month-old infants, the infants have shown quick habituation in (i) and (iii), but not in (ii). This suggests that infants over 4 months of age use a symmetrical cue to perceive the face.

◆ Exploration of top–down effects in the detection of faces

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Prior to recognising a face it is necessary to detect it. The process of face detection has been found to be influenced by a variety of visual properties of the image (Lewis and Edmonds, 2003 *Perception* in press). Two experiments are reported to establish whether this process is also influenced by higher-level processing (eg recognition) in either a top–down or interactive manner. The influence of facial familiarity, distinctiveness, and priming was explored. In contrast with the results with a face/jumbled-face decision, no effect of familiarity or distinctiveness was found for a face/non-face decision. Priming, however, was found to speed the face-detection decision, but only under certain constraints. We discuss how these results contribute to a fuller understanding of the (possibly distinct) processes of face detection and face recognition.

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◆ Priming effects on recognition of facial expressions

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In face recognition, the nature of a prime may affect the response time to the target face (Johnston and Barry, 2001 *Quarterly Journal of Experimental Psychology* 54 383–396). What will happen in the recognition of facial expressions? Can a prime affect it? We examined the effects of different types of prime on the recognition of facial expressions. The targets were prototypical expressions of happiness and unhappiness; and the primes were four types of expressions—identical, neutral, orthogonal (sleepy), and opposite facial expressions of the targets defined by an emotion space. The task was to judge the emotion (happy or unhappy) of the targets as quickly as possible. When the prime and the target were of the same person, there were significant effects of prime types on the response time for identifying emotions. But when the prime and the target were of a different person, the priming effects were not found. Our data demonstrate the influence of identity on the recognition of facial expressions. These results imply that two kinds of operations, visual processing and recognition, suggested in Bruce and Young's model (Bruce and Young, 1986 *British Journal of Psychology* 77 305–327) are not processed in a parallel and independent way.

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◆ Unconscious processing of facial expressions?

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Recent neuroimaging studies have suggested that discrimination of different facial expressions can occur without subjective awareness in the normal observers. In these studies, the facial expressions were typically limited to 30 ms in duration and masked by a neutral face to prevent awareness of the targets. The subjective awareness is reported on a binary (aware/unaware) scale.

To investigate the discrimination ability in relation to the reported awareness, we have carried out three experiments. Happy, fearful, angry, and neutral faces were briefly presented for 10, 20, 30, 40, and 50 ms and were masked immediately, either by a checkerboard pattern, a scrambled face, or a neutral face (mask duration 300 ms). Discrimination of facial expressions was carried out in a four-alternative forced-choice task. Participants also indicated their subjective awareness of the presented expression on a 9-point scale. Neutral faces were most effective at masking the target face, with chance-level discrimination of all expressions at 10 ms stimulus duration. Significantly above-chance discrimination was reported for stimulus durations ≤ 20 ms with better detection of happy faces than of anger or fear. Awareness ratings increased monotonically with increasing discrimination score, and were significantly higher at 20 ms than at 10 ms. Results indicate that conscious processing of facial expressions is possible at stimulus durations as brief as 20 ms, and that discrimination and awareness are highly correlated. Finally, there was no evidence suggesting that threat expressions, both anger and fear, were processed more quickly than positive expressions.

◆ **Lateralised repetition priming for face recognition: Priming occurs in the right hemisphere only**

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Repetition priming was used to examine possible hemispheric specialisations in face recognition. Participants saw a number of famous or not famous faces presented very briefly in either visual field, and had to decide whether each face was famous or not. After a short delay, the procedure was repeated with all faces presented centrally. All of the faces presented in the initial priming stage were presented again, together with a number of faces that had not been seen before. Again, participants had to decide whether each face was famous or not famous. Participants were unaware that the two phases of the experiment were related. Analysis compared mean reaction times to famous faces recognised in the second phase of the experiment, according to how they had been viewed in the first phase: presented to the left visual field (right hemisphere), presented to the right visual field (left hemisphere), or unprimed (not seen in the first phase). Faces initially presented to the right hemisphere were subsequently responded to significantly faster than those initially presented to the left hemisphere and those that were unprimed. There was no significant difference between the latter two conditions. Thus, faces that are presented initially to the right hemisphere, which is known to be specialised for processing faces, facilitate subsequent recognition, whereas faces presented initially to the left hemisphere provide no subsequent advantage. This experiment provides further evidence for right-hemisphere specialisation in face recognition and has potential implications for hemispheric distinctions in face memory.

◆ **Temporal characteristics of adaptation effects in the recognition of facial expression**

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The capacity for recognition of facial expression was investigated by using adaptation effects to measure identification performances on morphed expressions after exposure to various adapting faces. The faces depicted either fear, happiness, or sadness. For each emotional category, a range of six intensity levels (10%–60%) of morphs was generated by computer morphing procedures. The results showed that adaptation to a prototype emotional face impaired subsequent categorisation of the corresponding morphed expression. These adaptation effects were not affected by the delay between adaptation and categorisation. On the other hand, by manipulating the time course of the expression to be identified, differential adapting profiles arose. The importance of adaptation time found in further experiments is not compatible with higher cognitive functions being the sources of the effects. In general, this study demonstrates the utility of adaptation for revealing function characteristics and differential nature of facial-expression processing.

◆ **Adaptation to the facial expressions of emotion in the realistic face**

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It is a fundamental question whether facial expressions are processed categorically or continuously in the multi-dimensional space. In our previous study we examined this issue by means of the figural aftereffects induced by adaptation to facial expressions of emotion in the line-drawing face (Shibui et al, 2002 *Perception* 31 Supplement, 24). We replicated this experiment using realistic morphed faces. We measured the physical difference between the neutral facial stimulus and each of the four expressions and created opposite faces with reference to the neutral face [100% (original, eg happy), 50%, 0% (neutral), –50%, –100% (opposite, eg unhappy), for each

expression]. We followed the method of Leopold et al (2001 *Nature Neuroscience* 4 89–94) who showed the figural aftereffects for individual face identification. Subjects judged the expressions of 200 ms test faces following 5 s viewing of an adaptation face. In the control condition, subjects judged only test faces. The effects of adaptation were represented by the delays of response times between the control condition and the condition with adapt faces. Categorical conception hypothesises that the effects of adaptation are explained independently by the categorical rating of each expression. On the other hand, dimensional conception predicts that the effects of adaptation are explained by the relationship in the multi-dimensional space. The result suggests that the effect of adaptation is explained by the psychological distances between test faces and adapt faces in the semantic dimensions constituted by the pleasantness and activity. This is in line with the multi-dimensional model of face perception.

◆ **Estimation of the speed of object perception**

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The purpose of the study was to estimate the time needed to process complex objects for identification. An RSVP (rapid serial visual presentation) method was used. Ten facial images were shown in a rapid sequence on a computer display so that the duration of each image was equal and the images appeared immediately one after another. One of the images was a target face and the other images were distractor faces. The target in each sequence could be any of six possible targets with equal probability. A staircase algorithm was used to determine the threshold for the duration of images in the RSVP sequence, so that the probability of correct responses was 0.79. The threshold duration was determined as a function of image contrast. The results showed that threshold duration around 100 ms was sufficient for identification of target faces. The speed of face identification was independent of contrast at medium and high contrast values but decreased at low contrasts. Thus, the processing speed of face identification is largely contrast-invariant. This suggests that, at normal contrast levels, the factors that limit the speed of face identification do not depend on low-level signal-to-noise ratio in the visual system preceding face processing. At very low contrasts, however, the longer threshold duration may reflect longer temporal integration that is needed to increase the signal-noise-ratio at the level of face identification.

◆ **Impressions of facial expressions with asynchronous movement of facial parts**

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Temporal differences among moving facial parts are known to produce different impressions in laughter expressions and also when parts of a face move asynchronously in real facial expressions. The former results have been derived by using animation, and the latter from an analysis of photographs taken with a high-speed camera. In this study, the effect of asynchronous motion of facial parts on the recognition of smile was investigated by using photographic movies. Starting times of the movement of eyes and mouth were controlled in the facial expressions. The subjects evaluated the intensity and veridicality of each expression. When the eyes moved first and the mouth moved 10 ms after the eyes stopped moving, the intensity and the veridicality of the smile were both low; conversely when the mouth moved first and then the eyes moved 10 ms after the mouth stopped moving, the intensity of the smile was high but the veridicality was low. The latter result with respect to veridicality corresponded with the result derived from the animation experiment, but the former did not. These results suggest that when the time interval between the movement of facial parts is larger than that of natural smile, the expression is perceived as social smiling.

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◆ **Electrophysiological and behavioural analyses of cognitive processing implicated in the familiarity and emotional expression of faces**

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A behavioural and electrophysiological study was undertaken on the processes underlying facial recognition and their emotional expression. We asked whether identification and expression of faces operate in independent modules. Twenty-eight right-handed subjects performed two behavioural tasks: identification of familiarity and identification of expression, and fifteen of these were

evaluated for ERP characteristics. Four levels of familiarity (unknown, familiar, the subject's own face, and the face of the mother of the subject) and three types of emotional expression (disgust, neutral, smiling) were used. ERPs were recorded with 32 electrodes. There were three principal findings: (i) A familiarity effect appears for ERP activities at the post-stimulus interval between 170 ms and 400 ms. This effect is especially potent between very familiar faces on one hand and unknown faces on the other. This finding agrees with the hypothesis that familiarity modulates facial processing and suggests that the familiarity effect does not generalise to all familiar faces (Caharel et al, 2002 *International Journal of Neuroscience* **112** 1499–1512). (ii) The effect of emotional expression appears between 170 and 300 ms in the post-stimulus interval and its interaction with familiarity between 200 ms and 300 ms. (iii) A task effect was observed in terms of the modulation of the effects of familiarity and emotional expression. In particular, behavioural performances were correlated with ERPs only in the 'identification of familiarity' task. These results are discussed in terms of recent data on the expression (Pizzagali et al, 2000 *Clinical Neurophysiology* **111** 521–531), familiarity, and status of facial representations (Tong and Nakayama, 1999 *Journal of Experimental Psychology* **25** 1016–1035).

◆ Neurophysiological correlates of face gender recognition

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We investigated bioelectrical correlates of face gender recognition. Twenty healthy volunteers were enrolled (ten males and ten females; mean age \pm SD 24.1 \pm 3.5 years); all subjects were right-handed and heterosexual. Visual stimulation was performed with 64 pictures of human faces (32 of males, 32 of females) shown in random sequence on a PC monitor. EEG signals were recorded on the scalp with 32 electrodes placed in standard positions. Event-related-potential (ERP) signal evoked by female faces was subtracted from the signal evoked by male faces. EEG maps were calculated with the use of the Neuroscan program. Statistical analysis was performed with Student *t*-test ($p = 0.01$). We obtained three main results: (i) Viewing male and female faces evokes a differential EEG response of neurophysiological correlates of cognitive processes linked to face gender categorisation. (ii) There was an interaction between sex of the observer and sex of the target face. Significant differences in the ERP signal were detected in parietal and occipital regions of the scalp, with a latency of 140–210 ms for male subjects, and between 100–160 ms and 300–370 ms for female observers. (iii) There were differences in the lateralisation of these responses between the two sexes: when observing a female face, males activate the right hemisphere preferentially, while females activate the left one preferentially.

CLINICAL

◆ A pure case of achromatopsia following trauma with no observable cerebral lesions

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Patient NF, after a severe whiplash, was diagnosed severely achromatopsic. CAT and MRI brain scanning revealed no cortical lesions to visual or any other brain regions. Contrary to most cases of achromatopsia, there was no associated scotoma or agnosia. Six years after the trauma, we tested the patient extensively. Contrast sensitivity to equiluminant red–green gratings of low temporal frequency was deeply impaired, while visual acuity, perimetry, luminance contrast sensitivity for form and motion over a wide range of spatial and temporal frequencies were all perfectly normal. In a 'colour camouflage' task, NF performs better than controls (their performance was impaired by colour perception). Visual evoked potentials (VEPs) to equiluminant chromatic contrast gratings were absent, while those to luminance gratings were normal. These results indicate a selective loss of the chromatic contrast neural system at an early level, probably V1 or more peripherally, without any measurable anatomical effects. Present results show that sensitivity to chromatic contrast can be selectively damaged without altering any other visual performance.

◆ **Acquired colour-vision deficiency due to intracranial lesions**

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Type 3 (tritan) blue-colour defects are found in unilateral posterior hemisphere lesions, which cause hemianopic visual field defects, but there is no consensus whether these are found after injury to the right or left hemisphere or both [Birch, 2001 *Diagnosis of Defective Colour Vision* (Oxford: Reed Educational and Professional Publishing) p. 125]. We sought to characterise the dyschromatopsia in persons with hemianopic visual field defects, to determine the type and severity of colour defect and its relation to the right or left hemisphere damage. Computerised Farnsworth–Munsell 100-hue (F–M 100) test was used. Colour-vision testing data in eighteen persons with hemianopic visual field defects and a hundred controls were analysed. All of the statistics were calculated from the square root of the total and selective error scores. We used quantitative analysis of F–M 100 test error scores to determine the severity, the selectivity, and the type of dyschromatopsia. Ten persons with right and eight persons with left hemianopic field defects showed significantly worse total error scores on the F–M 100 test than controls ($p < 0.001$). The changes of the red–green selective scores in observers with hemianopic visual field defects were almost identical to the changes of the blue–yellow selective error scores. There was no significant correlation between the F–M 100 test total error scores in persons with right and left hemisphere damage.

◆ **Global and local perception of hierarchical stimuli in amblyopia**

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Amblyopia usually produces stronger deficits in linear acuity (letters in a line) than in single-letter acuity in humans. We examined the implications of this crowding effect for global and local perception of hierarchical stimuli. Compound shapes (small arrows pointing to the left or right embedded in large arrows) were presented to the normal and abnormal eyes of twelve anisometric amblyopes aged between 6 and 26 years. In two experiments, the compound stimuli were presented on a blank or a cross background, respectively, so that grouping by proximity (experiment 1) or similarity of shape (experiment 2) determined the perception of global structure. Reaction times (RTs) and response accuracies were recorded when subjects identified global or local shapes in separate blocks of trials. In both experiments, RTs were faster to global than local shapes for both the normal and abnormal eyes. However, the global RT advantage was larger for the abnormal than the normal eye. RTs were slower when global and local shapes were inconsistent than when they were consistent in experiment 2. This interference effect was stronger for the normal than the abnormal eye. The effects of amblyopia on perception of hierarchical patterns are discussed on the basis of these findings.

◆ **Visual attention in developmental dyslexia**

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Visual search tasks contain attentive and preattentive components and are well suited for the study of perceptual learning. Our purpose was to investigate whether schoolchildren diagnosed for developmental dyslexia show a selective visual attention deficit. Forty dyslexic subjects between 8.5 and 19 years of age and forty control subjects matched for age and gender were tested with methods of texture segmentation and visual search. The task of the subjects was to identify as rapidly and correctly as possible the location of an odd target amidst an array of distractors. The target could be an item differing from the distractors either by a single feature (form, colour, or orientation) or by a conjunction of features. Half of the subjects were tested with complex visual stimuli resembling reading material, the other half with items used in classical visual search. Numbers of errors and response latencies were recorded. Both groups of subjects showed significant improvements with age. In both groups, performance improved consistently from one test run to the next, indicating perceptual learning. The dyslexic children showed shorter latencies but elevated error rates for conjunction but not for feature search, when tested with stimuli similar to reading material. The two groups did not differ significantly when using canonical material. The differences between the two groups diminished with increasing age. We conclude that children with developmental dyslexia do not show a selective visual attention deficit. Their deficits seem to be specific for reading material. The possible role of hyperactivity on the accelerated processing of the complex conjunction tasks needs further investigation.

◆ **Distribution of visual attention: Evidence against impaired processing in developmental dyslexia on a simple cueing task**

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We investigated the distribution of visual attention in dyslexic adults using the cueing task of Facoetti and Molteni (2001 *Neuropsychologia* **39** 352–357). Nine dyslexic adults and eleven controls, matched for age and performance IQ, completed a battery of literacy/phonological tests. Attention was measured in a target-detection task by recording manual reaction time (MRT) in response to targets presented on a visual display. A cue circle (radius 4.5 deg) appeared concentrically to the central fixation point. After a variable SOA (150–300 ms), a target appeared randomly 3°, 6°, or 9° to the left or right (duration 20 ms). A high proportion of targets appeared within the circle. Participants were instructed to maintain central fixation throughout and eye movements were monitored with infrared oculography. While dyslexics were significantly impaired on literacy and phonological measures, there were no between-group differences on the attention task. ANOVA revealed a main effect of eccentricity on MRT, which increased with target eccentricity. No effect of visual field was observed, indicating a symmetrical distribution of attention in both groups. Also, no between-group differences emerged in the number of trials on which eye movements were made, and the number of eye movements made was not significantly correlated with MRT. Bivariate correlations revealed strong associations between phonology and literacy in both groups, such that higher single-word reading scores were accompanied by better phonological skills. No systematic pattern of correlations emerged between MRT and literacy performance. We conclude that poor phonological skills of dyslexics underpin their literacy difficulties and that in a simple cueing task their distribution of attention is normal.

◆ **Luminance and chromatic motion detection in dyslexia**

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Despite the fact that it has been established that developmental dyslexia is associated with multisensory deficits for the detection of dynamic stimuli, the mechanism underlying this deficit is still unknown. The most prominent, but also controversial, theory is the magnocellular-deficit hypothesis (Amitay et al, 2002 *Brain* **125** 2272–2285; Skottun, 2000 *Vision Research* **40** 111–127; Talcott et al, 2000 *Neuropsychologia* **7** 935–943). In our study, stimuli fitting the properties of either magnocellular or parvocellular channels were applied, so that the relative functioning of each channel was assessed. Two groups, thirty-seven dyslexic children and thirty-seven age-matched controls (mean age, 12 years) were analysed. Luminance motion detection was studied with a black and white RDK stimuli. Chromatic motion detection was analysed with red and green equiluminant RDKs. The equiluminant level of red and green stimuli was measured for each subject. The subjects were required to detect motion flowing in one of the eight directions. The signal-to-noise ratio decreased exponentially by 3 dB in each trial. To avoid tracking, each dot had a limited lifetime of 4 animation frames (duration, 200 ms). Significant differences were found between groups; in particular, dyslexics were found to have lower performance both in luminance and in chromatic motion detection. As expected, both dyslexics and controls had worse performance in chromatic motion detection. Since no interaction effect was found between groups and chromatic/luminance condition, the results are consistent with the magnocellular-deficit hypothesis in dyslexia.

◆ **Engagement of periventricular parieto-occipital regions in attention-demanding processing of biological motion**

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Recent findings in the primate brain (Bisley and Goldberg, 2003 *Science* **299** 81–86) and neuroimaging data in humans (Wojciulik and Kanwisher, 1999 *Neuron* **23** 747–764; Yantis, 2002 *Nature Neuroscience* **5** 995–1002) point to the involvement of parietal cortex in the generation of visual attention. Here, continuing the line of research on biological-motion processing in patients with early periventricular lesions (Pavlova et al, 2003 *Brain* **126** 692–701), we ask whether visual attention might be modulated already at the subcortical level. By using the simultaneous masking paradigm (Pavlova and Sokolov, 2000 *Perception & Psychophysics* **62** 889–899), a cohort of adolescents (aged 13–16 years) who were born preterm (at 27–33 gestational weeks) with different severity of bilateral periventricular leukomalacia (PVL) and two groups of matched controls (fullterms and preterms without PVL) were shown a set of point-light biological-motion stimuli. In a confidence-rating procedure, observers had to detect a prior-known point-light figure. Participants underwent a neuropsychological examination (HAWIK-III based on the WISC III). ROC analysis indicates higher susceptibility of patients to camouflage of point-light figure. In patients only, sensitivity correlates positively not just with the IQ factor PO (perceptual organisation), but also with PS (processing speed, which is based on visual attention tasks). Moreover, the sensitivity index, as well as the values of two IQ factors, decreases with increases in the volumetric PVL extent in the parieto-occipital complex. No relationship was found between these variables and the lesion extent in the frontal or temporal region. The data suggest that top-down processing of biological motion is closely related to visual attention. Most importantly, periventricular parieto-occipital regions might be recruited in deployment of the posterior attentional system.

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◆ **Spherical equivalent of myopia and contrast sensitivity**

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According to the clinicians, subjects with myopia up to 6 D and without any detectable changes in the ocular fundus are patients that have only a refractive disorder. This means that their visual performance can be made equal or close to that of the emmetropes simply by wearing the correct types of lenses. This view is also accepted by a number of visual researchers who have studied 'normal visual functions' in myopes with corrected-to-normal visual acuity. However, our previous data contradict this concept. Those data include evidence of decreased foveal sensitivity to negative contrast obtained for low-myopic subjects (−2.4 D) and the same to positive and negative contrast obtained for medium-myopic subjects (−6 D). The present investigation has been conducted particularly to study foveal sensitivity to contrast in myopes with larger in number and more homogeneous in structure value of spherical equivalent of myopia. The experiment included sixty myopes with a spherical equivalent of myopia ranging from 1 D to −7 D and twenty emmetropes, who were studied for their monocular contrast thresholds to positive and negative contrast at different photopic and mesopic conditions. Thresholds were determined through a change of the letter contrast by applying the staircase method and visual stimulus generator (Cambridge Research Systems). A comparison of data obtained for myopes with those for emmetropes reveals that further development of the myopia, even with 1 D only, causes a decrease in contrast sensitivity to both positive and negative contrast, and subjects with a spherical equivalent of myopia above −3.5 D display more abrupt changes in their contrast sensitivity, whereby their sensitivity to negative contrast decreases more than their sensitivity to positive contrast.

◆ **Light scattering effect on visual response to colour stimuli**

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We have modelled a situation similar to scattering in an eye affected by a cataract. A polymer dispersed liquid crystal (PDLC) cell was placed in front of patients' eyes. Light scattering in such

a cell can be continuously controlled by applying pulsed bipolar voltage up to 30 V, thus bringing the cell from an opaque light-scattering state to transparent state. First, human visual response tests at a distance of 3 m were performed by simulating on the computer screen Landolt C quasi-monochromatic stimuli—R, G, and B phosphors. Second, we carried out contrast sensitivity tests with the same colour Gabor patterns, displaying them on the computer screen. Experiments were performed in a darkened room to eliminate background light scattering. Finally, we determined flicker fusion frequency with colour stimuli, using blue, green, and red light-emitting diodes. Light scattering induced by a PDLC cell very efficiently lowers the visual acuity for blue Landolt C stimuli. With one such cell, the visual acuity decreased down to 0.6 (decimal), and with two cells down to < 0.4 . The acuity for white stimuli was weakly affected, and that for monochromatic red Landolt C stimuli practically did not change as compared with the case of the cell in the transparent state. The contrast sensitivity, however, decreased for all R, G, and B Gabor stimuli, to the greatest extent for short-wavelength and high-spatial-frequency patterns. Similar experiments on patients with eyes affected by real cataracts are in progress, to allow us to evaluate the ability of such controllable scattering cells to simulate the visual performance of eyes affected by cataracts. [Supported by EU Excellence Centre Program Project CAMART.]

AUTHOR INDEX

Note: de X, van X, van den X, von X, and similar are all indexed under X

- Actis-Grosso R** 151a
Adini Y 30b
Aghdaee S-M 146a
Agostini T 11b, 41a, 51c, 150a, 151c
Ahissar M 32c, 132b
Ahumada A J 37b
Aivar M P 66b
Akarun L 1b
Akutsu H 82c
Alais D 9a, 44b, 96b
Alcalá-Quintana R 156b
Alexeenko S V 76b, 166c
Alleysson D 146b
Alpaydin E 1b
Amano K 110b
Amit D 93a
Andersen G J 73a
Anderson R S 39a
Ando H 97b
Andrews T J 59a
Anker S 7a
Annan V J Jr 52a
Anstis S 50c
Arcara G 163b
Arcizet F 171b
Arguin M 120b
Arndt P A 8b
Arnold B E 79c
Arnold D H 46c, 164a
Arrighi R 96b
Asakura N 75b
Ashida H 97b, 106b
Aslin R N 90b
Atkinson J 7a, 49b
Auckland M E 43a
Auvray M 94a
Avitable M 25a
Aymoz C 143a
Bachert I 176c
Bachmann T 126c
Baciu M 67c
Bacon N 170a
Badcock D R 144c
Baddeley R J 51a, 55a
Baillet G 149a
Banks M S 81a
Baraas R C 147b
Barbieri-Hesse G S 158c
Barbur J L 158a
Barlasov A 127b
Barlow H 31a
Barnett A 7a
Barras H J 72c
Barraza J F 144a
Barrett D J K 136b
Barth E 109a
Barthaud J 134a
Barthélemy F 110a
Bartoletti A 57a
Bateson E V 56a
Batty M J 134c
Baud-Bovy G 88b
Baumberger B 70b, 72c
Bavelier D 16a
Bayerl P A J 19c
Baylis G C 18a
Baylis L L 18a
Beard B L 37b
Beauvillain C 24c, 111c
Bedingham S 104c, 105a
Bekkerling H 65c
Belle G van 127c
Belli V 177b
Benassi M 177b
Berg A V van den 13b
Bernacchia A 93a
Bernard C 164b, 174c
Bernardis P 10b
Bertamini M 19a, 145a
Berthoz A F 16b, 69c
Bertin R J V 69c
Bertulis A 125b
Beykirch K 99a
Bharadwaj S R 108b
Bielskute B 176a
Bimler D L 85c
Bini G 124c
Birbaumer N 178a
Birtles D 7a
Bisio G M 12a, 12c
Blackaby L 103a
Blake R 19b
Blakemore C 139a
Bloj M 41b, 42a
Blundo C 175b
Bodis-Wollner I G 25a, 25b
Bolzani R 177b
Bompas A 64a
Bonnar L 140a
Bonneh Y S 9c
Borghetti D 1a, 75a
Born R T 20a
Boucard C C 53a
Bouet R 39c
Bourne V J 173a
Boutsen L 118c
Boxtel J J A van 62b
Braddick O J 7a, 49b
Bradshaw M F 110c, 143b
Brainard D H 41b, 42a
Brenner E 11a, 20c, 66b, 72a, 109c
Bressan P 151a, 152c
Bressanelli D 115b
Bross M 88a
Brosseau-Lachaine O 86c
Brouwer A 62a
Brugger P 126b
Bruno A 65c, 100b
Bruno N 8a, 10b, 145a
Buckley D 14a
Buckthought A 83a
Bühmann T 70a
Buffat S 81b
Bulatov A 125b
Bullet G 88a
Bullier J 171b
Bülthoff H H 62a, 99a, 116c, 117a, 117b
Buron V 67c
Burr D C 9a, 44b, 96b, 102a, 175b
Burt D M 57b
Butler S H 37a, 57b
Caharel S 174c
Campana G 163b
Caravolas M 177a
Carrasco M 131c
Casco C 103b, 163b
Casile A 143c
Castellarin I 151c
Castelli S 59b
Castet E 110a, 112c
Caudek C 74b, 74c
Cavanagh P 1a
Cave K R 43a, 134c
Cellerino A 57a, 175a
Chai Y C 44a
Chanderli K 72c
Charron C 64b
Chauvin A 158b
Chen I 130c
Chen K 44c
Chen V J 144a
Chen Y 27a, 121a
Cheong L-F 11c
Chihman V N 122a
Chiorri C 124c
Chou W 133b
Chu W 141b
Chua F K 116b, 139b
Chueva I V 90a
Chugg C 50a
Chung C 172c

-
- Claessens P M 25c
 Clark S A 125a
 Clarke T J 143b
 Clifford A 87b
 Clifford C W G 26b, 124b
 Cole G G 36c
 Collignon O 9b
 Collins T 111c
 Collomb K 67c
 Cook N D 126b
 Cornelis E V K 85a, 118a
 Cornelissen F W 53a, 65b, 109c
 Cornilleau-Peres V 11c
 Costall A 83b
 Cottrell G 56b
 Cowey A 36c
 Creanga D E 166b
 Crespi S 65c, 100b
 Csatho A 127a
 Culham J C 15b
Dahl C 117b
 Damme W J M van 37c
 Daniell A 103c
 Danilova M 160c
 Danti S 102a
 Darcheville J-C 68b, 98b
 Dasara M 125c
 Dattani R 48c
 Daugirdiene A 157a
 Davies I R L 87b
 Davis H 73c
 Debruyne P 98b
 Defoort S 98b
 De Lillo C 59b
 Del Viva M 102a
 Demeyer M 119a
 Dennis J 95a
 Deshkovich A 122a
 Deubel H 113a
 De Volder A G 9b, 36a
 De Winter J 118b, 119c, 139c
 Diamond M 175b
 Di Luca M 74b
 DiMase J S 104b
 Ding J 14b
 Di Russo F 175b
 Dodds C M 92c
 Domini F 74b, 74c
 Dong T 132a
 Donnelly N 43a, 120a
 Donner T H 120a
 Doorn A J van 82b, 85a, 118a
 Doré Mazars K 111c
 Dornhoefer S M 140b, 169b
 Doshier B 4a, 141b
 Dosualdo P 11b
 Doumen M J A 84b, 84c
 Downing P E 92c
 Doyle L 88a
 Dresp B 134a, 160a
 Drewes J 109a
 Driver J 15c, 22b
 Droll J A 6c
 Droulez J 11c
 Dudkin K N 90a
Eckstein M P 44c, 140c
 Economou E 42b
 Edelman S 34c
 Edgar R 73c
 Edmonds A J 172b
 Ee R van 13b, 45b
 Ehrenstein W H 79c, 135c, 148b
 Eimer M 15c
 Ejima Y 161c
 Elkin J 93b
 Elst J van 37c
 Engles M P 89c
 Enriquez A J 73a
 Erkelens C J 20b
 Es J van 53a
 Eskew R T Jr 39b
 Estaún S 106a
Fahle M 29a, 115a, 116a
 Fantoni C 125c
 Fauquet J 106a
 Felisberti F M 156c
 Festman Y 132b
 ffytche D H 168a
 Field D T 143b
 Filley E T 78a
 Fine E M 88c
 Fiorentini A 175b
 Fischer M H 10a
 Fiser J 90b
 Flückiger M V 70b, 72b, 72c
 Foreman N 122a
 Forgacs P 25a
 Foster D H 110b, 147b
 Fowlkes C C 55b, 171a
 Franke R 169b
 Franklin A C 87b
 Fransens R 127c
 Franz V H 62a
 Freeman T C A 13a
 Frégnac Y 30a
 Frenz H 70a
 Frisby J P 14a, 73c
 Fuggetta G 163b
 Fujisaki W 8c
 Fukui T 61b
Gaber T J 169b
 Galmonte A 11b, 51c
 García-Pérez M A 156b
 Gautier V 107c
 Geeraert J 94b
 Gegenfurtner K R 40a, 91b, 142a
 Gellatly A 134b, 161a
 Gentaz E 88b, 98b
 Georgeson M A 46b, 158c
 Gepshtein S 22a
 Gérardin P 52b
 Gerbino W 89a
 Geusebroek J 54a
 Giese M A 34c, 143c
 Gilbert C D 30c
 Gilchrist A L 42b, 152a
 Gilchrist I D 37a, 57b
 Gillam B J 27b
 Gilroy L A 19b
 Gimenez-Sastre B 106c
 Giordano B L 152c
 Girard P 171b
 Giraudet G 149a, 169a
 Girshick A R 81a
 Gizycki H von 25a
 Gobell J 45a
 Goddard P A 103a, 123b
 Godfroy M 94b
 Goebel C 176c
 Gokberk B 1b
 Goltz H 21b
 Goodale M A 15b, 21b
 Gool L van 127c
 Gorea A 5a, 17a, 67a
 Gosselin F 56b
 Goto A 73b
 Goutcher R 124a
 Graf M 117a, 117b
 Grainger J 121b
 Greenlee M W 25b
 Greenwald S H 41b, 42a
 Gregory R L 51b
 Grieco A 103b, 154a
 Grigorescu C 1c
 Grodd W 178a
 Groeger J A 110c
 Grünau M von 107b
 Grzywacz N M 144a
 Guyader N 158b
 Gvozdenović V 153c
Hache J-C 98b
 Haggard P 23a
 Häkkinen J 75a, 131b
 Hamada J 135c
 Hamburger K 155b
 Hamer R D 38a
 Hamilton G 123b

-
- Hammett S 104c, 105a
 Hampson S E 143b
 Han J 172c
 Han S 59c, 176b
 Hanneton S 94a
 Hannus A 65b
 Hansen T 40a
 Harashima H 173c
 Harrar M 149a
 Harris C 128a
 Harrison S J 163a
 Harvey M 37a, 57b
 Hashimoto F 98a
 Hauck R E 41b, 42a
 Hawken M J 101b
 Hay J L 138a
 Hayashi M 98a
 Hayashi T 97c
 Hayhoe M M 6c
 Haynes J D 48b
 Heard P F 50a
 Heeley D W 125a
 Heil M 128a
 Heinke D 18c
 Hellmann A 121c
 Helmert J 140b
 Hemeren P E 142c
 Hérault J 146b
 Hershler O 57c
 Herzog M H 115a, 116a
 Hesselmann G 138a, 139a
 Heywood C A 36c
 Hibbard P B 75c
 Hill H 56a
 Hillstrom A P 44a
 Hirose M 68a
 Hita E 80a
 Hochstein S 32c, 57c, 93a, 120c, 127b
 Hock H S 102b
 Hoellen N 10a
 Hofbauer M M 96a
 Hogervorst M A 37c
 Holcomb P J 121b
 Holcombe A O 26b
 Hole G J 173a
 Holloway R 89c
 Hong J 95a
 Hongler M 167b
 Hooge I T C 37c, 109b, 111b
 Horowitz T S 104b
 Hsu L 129a
 Htwe M T 80c
 Hubbard T L 145b
 Huber J W 121c
 Huckauf A 6b
 Hulleman J 123c
 Humphrey G K 15b
 Humphreys G W 18b, 18c, 123c
 Hurlbert A C 129b
 Hurri J 54b
 Hutchinson C V 101c
 Hutchinson S J 147a
 Hyvarinen A 54b
 Ibanez V 154c
 Ichihara S 82c
 Idesawa M 77b, 77c, 80b, 80c
 Intskirveli I E 149b
 Inui T 61b, 61c, 63b, 97c
 Isono K 174b
 Israël I 63c, 69c
 Ito H 67b
 Iverson P 9c
 Izawa K 173c
 Jacomuzzi A 8a
 Jacot J 167b
 James T W 15b
 Jankauskienė J 176a
 Janković D 97a
 Jaschinski W 79c
 Jaskowski P 135a
 Jeanjean S 112c
 Jentzsch I 93b, 140a
 Jiang Y 59c
 Jiménez J R 80a
 Jiménez del Barco L 80a
 John A 78b
 Johnston A 46c, 164a
 Johnston R A 172b
 Jones E 57b
 Joos M 113c, 140b
 Jouffrais C 171b
 Judge J 177a
 Jupe J R 129c
 Kagan I 76c
 Kahana M 5b
 Kamitani Y 165a
 Kanai R 79a, 100a, 155a, 165a
 Kanazawa S 86a, 86b, 87a
 Kanda Y 95b
 Kaneko H 153b
 Kaping D 117a
 Kappers A M L 84b, 84c, 153a
 Kashi R 95a
 Kashino M 8c
 Kavanagh E 7b
 Kawahara T 92a
 Kayahara T 68a
 Keeble D R T 163a
 Kentridge R W 36c
 Kerzel D 64c
 Keus I M 66a
 Kezeli A R 116a, 149b
 Khang B 153a
 Khuu S K 144c
 Kikuchi A 71a
 Kikuchi R 71a
 Kim H J 69a
 Kim J 133a
 Kim M 172c
 King A J 15a
 Kirchner H 24c, 170a
 Kiritani Y 69a
 Kirkland J 85c
 Kitagawa N 82c
 Kitaoka A 106b
 Kitazaki M 68a, 73b
 Kloth N 10a
 Knoblauch K 39c, 52b, 146c
 Knox P C 10b, 114b, 177a
 Koch C 113a
 Koenderink J J 2b, 84a, 84b, 84c, 153a
 Koenig O 67c, 134a
 Kogo N 127c
 Kojo I V 111a
 Kolesnik M 70a
 Komidar L 144b
 Komitov L 178c
 Kontsevich L L 58a
 Korenuks D 178c
 Kovács G 136a
 Kozachenko A 178c
 Kozawa R 114a
 Krägeloh-Mann I 178a
 Kramer P 129a
 Krasilnikov N N 166a
 Krasilnikova O I 166a
 Kristjansson A 22b
 Kubota M 92a
 Kubovy M 22a
 Kung E 25a
 Kwak Y 38b
 Laarni J 131b
 Labbani-Igbida O 64b
 Lalanne C 64d, 106c
 Lalonde R 164b, 174c
 Laloyaux C 9b
 Lamb T D 38a
 Lamberts K 118c
 Lange J 34b
 Langer M S 21a
 Lankheet M J M 100a
 Lappe M 34b, 70a, 112a, 142b
 Lappin J S 18b
 Laurinen P I 40b, 152b, 159a, 159b, 165c
 Lawson R 116c

-
- Lebedev D S 148a
 Lecoq C 63c
 Le Dantec C 164b
 Ledgeway T 101c
 Lee S 77a
 Leek E C 119b, 120b
 Leeuwen C van 114c
 Legargasson J F 107c
 Lennert T 155b
 Leo F 102a
 Leonards U 51a, 154c
 Leopold D A 115c, 137c
 Leumann L 126b
 Leuthold H 93b, 140a
 Lewis M B 172b
 Li A 12b
 Li W 30c
 Liao B 176b
 Liao H 133c
 Liebman P A 38a
 Lier R van 127a
 Likova L T 74a
 Lillo C De 59b
 Ling Y 129b
 Lingelbach B 148b
 Lingnau A 108a
 Liu L 176b
 Liu Z 33b
 Lo S 135b
 Logan S P 172d
 Logothetis N K 32a, 115c, 137c
 Logvinenko A D 40c, 147a
 Lopez-Moliner J 20c
 Lorenceau J D 64d, 81b, 106c
 Lotto R B 59a
 Lu Z-L 4a, 141b
 Ludwig E 128a
 Ludwig C J H 37a
 Lukauskienė R 176a
 Lussanet M H E de 142b
 Luyat M 68b, 98b
Maas H L J van der 102b
 Macaluso E 15c
 McCann J J 151b
 McConkie G W 24a
 McCourt M E 95c
 McDonald J S 170b
 MacDonald L W 38b
 McEwan W 47b
 Macknik S L 49a, 60a
 McMullen O 101a
 McOwan P W 46a
 McSorley E 23a
 Magnussen S 130b
 Maguire R P 53a
 Maiche A 106a
 Maier A 115c
 Majaj N 90c
 Malik J 55b, 108b, 171a
 Malmberg K 4b
 Mamassian P 124a
 Marcilly R 68b
 Marendaz C 88b, 158b
 Marino B F M 65a
 Marković S 97a, 153c
 Martin D R 55b, 171a
 Martin R 168c
 Martinetz T 109a
 Martinez-Conde S 49a, 60a
 Martinez-Trujillo J C 3b
 Marx J 24b
 Massironi M 115b
 Masson G S 110a, 112c
 Mather G W 103c
 Matsumiya K 153b
 Matsumoto E 160b
 Ma-Wyatt A 6a
 May K A 46b
 Medina J 80a
 Meese T S 48c
 Meijer W 109c
 Meinhardt G 26a, 89b, 162a, 162b
 Mel B 91a
 Melcher D 100b, 112b
 Menegaz G 146c
 Meneses Y L de 167b
 Mennucci A 57a
 Merkuliev A 122a
 Merzenich M M 9c
 Meyer G F 96a
 Michels L 112a
 Mihaylova M 39a
 Milders M 137b, 138a, 139a, 172d
 Milner A D 15b
 Minini L 61a
 Misaki M 160b
 Misawa Y 71a
 Mitha K 41b, 42a
 Miura K 126a
 Miyauchi S 160b
 Mochizuki T 95b
 Mogi K 77b
 Mollon J D 160c
 Monaci G 146c
 Monot A 83c
 Montanaro D 48a, 53b
 Montaser Kouhsari L 58b
 Morgan M J 47a, 47b, 78b, 156c
 Mori G 108b
 Morikawa K 91a
 Morrone C M 44b, 48a, 53b, 65c, 112b, 175b
 Mortensen U 89b
 Morvan C 63a
 Mosca F 145a
 Mouaddib E M 64b
 Muir K 37a
 Mulligan J B 23b
 Murri L 175a
 Müsseler J 113b
Naik P 48c
 Naji J J 13a
 Nakayama M 98a
 Náñez J E Sr 89c
 Nascimento S M C 110b
 Näsänen R E 149c, 174a
 Neo G 116b
 Neri P 43b
 Neumann H 19c
 Neustadt B 148b
 Nicholas S C 38a
 Niedeggen M 128a, 137b, 138a, 139a
 Nikolaev A R 114c
 Nishida S 8c, 46c, 164a
 Noe A 33a
 Noël M 98b
 Noest A J 13b
 Noguchi K 69a
 Norris B 44a
 Nuding U 170c
Oda M 174b
 Oezyurt J 25b
 Ogawa K 61c
 Ogi T 68a
 Ogris G 54c
 Ohmi M 75b
 Oja A 126c
 Ojanpää H M 149c, 174a
 Ojéda N 67c
 Oka S 161c
 Okajima K 69b, 71b
 Olzak L A 159a, 159b, 165c
 Ons B 118b
 O'Regan J K 33a, 64a, 92b, 94a
 Orlov T 93a
 Osaka M 93c
 Osaka N 93c
 Otsuka Y 86b, 87a, 172a
 Otte T 164c
 Otto T 116a
 Over E A B 109b
 Oxtoby E K 147b
 Oyama T 85b
 Ozolinsh M 178c
Pack C C 20a
 Paffen C L E 79a, 79b

-
- Paletta L 54c
 Palmer J 4c
 Palsdottir S 142c
 Pannasch S 24b, 113c
 Papathomas T V 95a, 136a
 Paramei G V 135c
 Park J 133a
 Parovel G 83b
 Párraga C A 51a, 168b
 Parton A 120a
 Pas S F te 79a, 79b
 Pasieka B 95c
 Paul I 164b
 Pauli P 134c
 Pavlova M 105b, 178a
 Pearson J 26b, 124b
 Peh C-H 11c
 Pei F 9c
 Pelli D G 3c, 90c
 Perge J A 100a
 Perna A 48a, 53b
 Peromaa T L 40b, 152b
 Pérot J C 169a
 Perrett D I 57b
 Persike M 26a, 162a
 Petit J-P 121b
 Petitot J 2c
 Petkov N 1c
 Peyrin C 158b
 Pichereau T 83c
 Pilling M 161a
 Pinna B 125c
 Pins D 168a
 Pinto P D 110b
 Plantier J 169a
 Ploeger A 102b
 Pöder E 141a
 Podlesek A 144b
 Polat U 29c
 Porter G 156a
 Pos O da 154b
 Pouget P 24c
 Prior H 155b
 Przybyszewski A W 76c
 Puhakka M 131b
 Puts M 127a, 161b
 Pylyshyn Z W 16c
Racheva K 39a
 Rainville S J M 104a
 Rajimehr R 45c
 Ray E 123a
 Rebai M 164b, 174c
 Rees G 48b
 Reeson R 7a
 Renier L 9b
 Reppa I 119b, 120b
 Richters D P 39b
 Riddett A 87b
 Riddoch M J 18b
 Riecke B E 99a
 Righi G 11b, 51c
 Ripamonti C 41b, 42a
 Rizzi A 151b
 Rogers B J 50b
 Röhrbein F 96a
 Roinishvili M O 149b
 Rolke B 128a
 Roncato S 154a
 Rorden C 17c, 18a
 Rosas P 162c
 Rose D 136b, 143b
 Ross D A 40c
 Ross J 6a
 Rothert A 169b
 Roumes C 81b, 94b, 169a
 Rozhkova G I 87c
 Rudd M E 52c, 150b
 Ruppel S E 145b
 Ruppertsberg A I 19a
 Rutschmann R M 25b
 Rydberg A 177b
Saarela T P 159b, 165c
 Sabatini S P 12a, 12c
 Sagi D 5a, 17a, 30b
 Sahraie A 36b, 137b, 138a, 139a, 172d
 Saida S 70c, 71b, 114a
 Saidpour A 73a
 Sakurai K 71a
 Salmela V R 40b, 152b
 Salminen N H 111a
 Sanborn A 4b
 Sander D 67c
 Santella D 131c
 Sarris V 155b
 Sartucci F 175a
 Sasaki Y 89c
 Sauer C W 73a
 Sawada T 153b
 Saylor S A 159a
 Schaub M J 70b
 Scherlen A-C 107c
 Schill K 96a
 Schlottmann A 123a
 Schmidt M 26a, 162b
 Schmidt O 148b
 Schmidt T 66c
 Schmonsees U 115a
 Schor C 108b
 Schwarz W 66a
 Schyns P 56b
 Scocchia L 65a
 Scott-Brown K C 125a
 Scott-Samuel N E 104a, 131a
 Segawa K 70c, 71b
 Segebarth C 67c
 Seghier M 154c
 Seiffert A E 35c
 Seitz A 89c
 Sekuler R 5b
 Selesnick I 25a
 Serrano-Pedraza I 165b
 Shadlen M N 4c
 Sharikadze M 116a
 Shelepin Y E 122a, 166a
 Sherwood A C 46a
 Shibata I 67b
 Shibui S 173c
 Shiffrin R M 4b
 Shigemasu K 173c
 Shimajo S 8c, 31b, 155a
 Shimozaki S S 44c, 140c
 Shioiri S 77a
 Shirai N 86a, 86b, 172a
 Shkorbatova P Y 76b
 Shneur E 120c
 Shyu S 173b
 Sierra-Vázquez V 165b
 Sigman M 30c
 Sikl R 82a
 Silva M M 110c
 Simecek M 82a
 Simola J M 111a
 Sinha P 2a
 Sinico M 82b
 Sireteanu R 176c
 Skalska B 135a
 Skarratt P A 134b
 Smagt M J van der 79a, 79b
 Smeets J B J 11a, 20c, 66b, 72a, 111b
 Smeulders A W M 54a
 Smith M L 56b
 Smith W S 157b, 170b
 Snodderly D M 76c
 Snowden R J 7b
 Sohn W 95a, 136a
 Sokolov A 105b, 178a
 Solari F 12a, 12c
 Solomon J A 47a, 47b, 78b, 156c
 Soranzo A 41a
 Souman J L 22c
 Spang K 29a
 Spehar B 122b
 Sperling G 14b, 45a
 Spillmann L 155b, 164c
 Spinelli D 175b
 Spinozzi G G 59b
 Sponga M 154b
 Stanikunas R 157a
 Staudt M 178a
 Steingrimsson R 90c

- Stelmach L B 83a
 Stentiford F W M 137a
 Stine W W 78a
 Stockdale C R 107a
 Stoimenova B D 178b
 Stroganov V 125b
 Stucchi N 65a
 Sugio T 61c
 Sullivan B T 6c
 Süssstrunk S 52b, 146c
 Svegzda A 157a
 Sweeting L 129b
 Swezey A 3c
 Syed A 25a
 Tadin D 19b
 Tadmor Y 157b, 168c, 170b
 Takase M 69b
 Talgar C 131c
 Tallon-Baudry C 92b
 Tan W P 116b
 Tanaka Y 160b
 Tanskanen T 174a
 Tanzilli P 175b
 Taraborelli D 27c
 Tatler B W 55a
 Taya S 126a
 Taylor J 43c
 Théry V 98b
 Thibault D 86c
 Thomas C 21b
 Thompson P G 104c, 105a
 Thornton I M 34c, 62a
 Thorpe S J 32b, 170a
 Timmann-Braun D 29a
 Tokareva V S 87c
 Tolhurst D J 51a, 168b
 Tommasi M 142a
 Tong F 167a
 Toporova S N 76b, 166c
 Tosetti M 48a, 53b
 Tosten P 83c
 Town C 55c
 Tozawa J 85b
 Tranchina D 38a
 Tranduy D 9b
 Treue S 3b
 Trevethan C T 36b
 Triesch J 6c
 Troncoso X G 60a
 Trościanko J 51a
 Trościanko T 51a, 154c, 156a, 168b
 Tse P U 35b
 Tseng C 45a
 Tsodyks M 30b
 Tsubomi H 93c
 Tyler C W 58a, 74a
 Tzvetanov T 160a
 Uchida J 76a
 Uchida M 77c
 Uemura Y 69a
 Ujike H 70c, 71b, 114a
 Ukibe T 69b
 Ukkonen O I 131a
 Usher M 120a
 Vaitkevičius H 157a
 Vallines I 25b
 Vandenbroucke M W G 22b
 Van den Dobbelsteen J J 72a
 Vanlierde A 9b, 36a
 VanRullen R 132a
 Van Velzen J 15c
 Vassilev A G 39a
 Vayrynen J 54b
 Velde C van de 107b
 Velichkovsky B M 24b, 113c, 140b, 169b
 Veraart C 36a
 Vergilino Perez D 111c
 Verhulst F 139c
 Verleger R 135a
 Verstraten F A J 79a, 79b, 165a
 Vidal Miranda J R 92b
 Vidnyánszky Z 136a
 Viénot F 149a
 Vignali G 56a
 Viliunas V 176a
 Vishwanath D 81a
 Vital-Durand F 86c
 Vitu F 24c
 Viviani P 143a
 Vlaskamp B N S 109b
 Vogt J 155b
 Vogt S E 130b
 Volder A G De 9b, 36a
 Vorberg D 66c
 Vuilleumier P O 17b
 Vuong Q 74c
 Wade A R 74a
 Wade N 101a
 Wagemans J 25c, 82c, 118b, 119a, 119c, 127c, 139c, 162c
 Wagner M 128b
 Walker L 55b, 108b
 Walker R 23a
 Walkey H C 158a
 Walter S 91b
 Wanet-Defalque M-C 36a
 Wang K 176b
 Wang Q 39b
 Waszak F 67a
 Watanabe T 29b, 76a, 89c
 Wattam-Bell J 7a, 61c
 Weert C de 161b
 Werner A M C 148c
 Werner I 176c
 Wertheim A H 22c, 34a
 Westenberg M A 1c
 Wexler M 62b, 63a
 Wezel R J A van 100a
 Whitney D 21b
 Wilke M 137c
 Willems B 82b
 Williams P 131c
 Wilson S 103a, 123b
 Winawer J 99b
 Witthoft N 99b
 Wolf R 130a
 Wolfe J M 104b
 Wu D-A 155a
 Wuerger S M 19a, 96a
 Wurfel J 144a
 Yaguchi H 77a
 Yakovlev V 93a
 Yamaguchi M K 86a, 86b, 87a, 172a
 Yamamoto Y 98a
 Yanagida T 161c
 Yang S 24a
 Yeh S 27a, 121a, 129a, 133b, 133c, 135b
 Yoshida C 63b
 Yoshida T 93c
 Yoshino T 68a
 Yoshizawa T 92a, 101b
 Zaenen P 119a, 162c
 Zaidi Q 12b
 Zandvakili A 100c
 Zanker J M 43c
 Zavagno D 52a, 152a
 Zdravković S 150a
 Zemach I K 150b
 Zetsche C 96a, 170c
 Zhang H 80b
 Zhang L 21a
 Zhang Q 77b
 Zhou F 5b
 Zlatkova M 39a
 Zohary E 93a
 Zucker S W 3a
 Zur D 30c